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**A RE-ASSESSMENT OF THE TELMATOBIINE  
LEPTODACTYLID FROGS OF PATAGÓNIA**

By  
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As presently constituted, the leptodactylid frog genus *Telmatobius* contains some 30 species distributed on the Andean cordilleras from Ecuador (0° 15' N) to southern Argentina (ca. 43° S). The species from Bolivia, Ecuador, Perú and from northern Argentina and Chile are Andean frogs whereas those from southern Argentina include Andean and extra-andean species. Although known for only the past decade, the generic relationships of these southern species are the subject of considerable uncertainty. My characterization of the genus (Lynch, 1971) was incomplete in that only three species were available for study; even so, considerable heterogeneity was evident. The unusual species of that limited sample was *T. patagonicus*, the first of the Patagonian species described.

Six Patagonian species are now known from Neuquén and Río Negro Provinces, Argentina, and a seventh was recently described from southern Chile (ca 49° S). The relationships of these species with other telmatobiine leptodactylids are obscure. The seven species are variously assigned to three genera. Initially, my study was to be one of the seven "extra-andean" species but it soon became evident that their relationships were not so close to the Andean *Telmatobius* (and allied genera) as might be surmised from perusal of the literature. The study was further enlarged by the fortuitous availability of several rare and/or recently described Argentine and Chilean telmatobiines. The availability of these frogs prompted a re-assessment of the relationships and proposed classification of *Alsodes*, *Eupsophus*, *Insuetophrynus*, and *Telmatobufo*, as well as a

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re-evaluation of the putative tribes Alsodini, Batrachylini, and Telmatobiini of the leptodaetylid subfamily Telmatobiinae.

The extra-andean assemblage of *Telmatobius* consists of seven species: *grandisonae* Lynch, *nitoi* Barrio, *patagonicus* (Gallardo); *praebasalticus* Cei and Roig, *reverberii* Cei, *solitarius* Cei, and *somuncurensis* Cei. This assemblage of frogs is distributed south of 39° in patagonian South America (Fig. 1).

In an attempt to re-evaluate the relationships and classification of the telmatobiine leptodaetylid frogs of Patagónia, I have first reviewed the morphology and taxonomy of the seven Patagonian *Telmatobius*. Secondly, I have expanded our knowledge of the osteology of the several Patagonian genera heretofore poorly known. Following this review, I present an analysis of the taxonomic characteristics used for the lower telmatobiines. This analysis forms the basis for an analysis of the relationships of the various genera. In the concluding discussion and summary, I provide a biogeographic rationale and propose a classification that reflects my current understanding of the relationships of the genera of this leptodaetylid stem group.

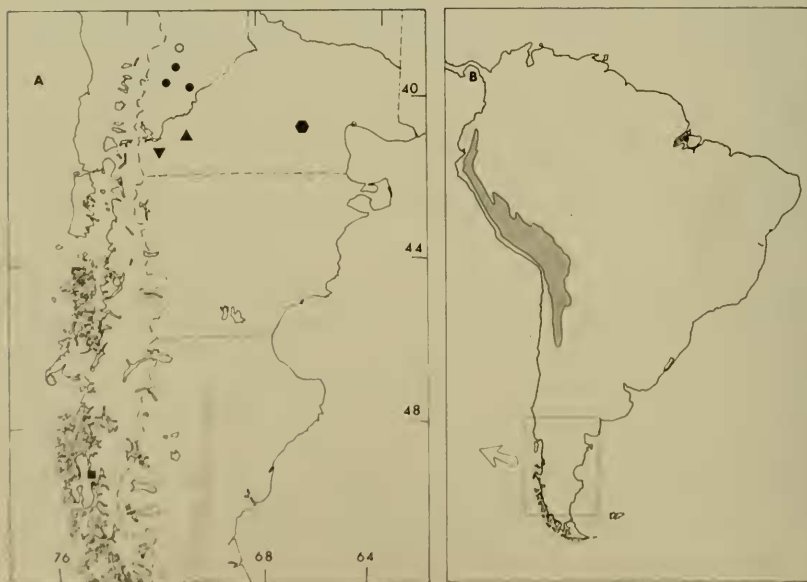


FIG. 1.—(A) Distribution of *Atelognathus*: *A. grandisonae* (square), *A. nitoi* (triangle), *A. patagonicus* (all circles), *A. praebasalticus* (open circle), *A. reverberii* (hexagon), and *A. solitarius* (inverted triangle). (B) Distribution of *Telmatobius* (*sensu stricto*).

THE PATAGONIAN *Telmatobius*

Gallardo (1962, 1970) placed *patagonicus* in *Batrachophrynus*, an assignment contested by Cei (1970a), Cei and Roig (1968), and Lynch (1971). The other six species were described as *Telmatobius* species (Barrio, 1973, Cei, 1969a, 1970a, Cei and Roig, 1968, and Lynch, 1976), but Gallardo (1970) assigned *praebasalticus* and *reverberii* to *Alsodes*. Lynch (1971, 1972) questioned the propriety of separating *Alsodes* and *Eupsophus* and placed *praebasalticus* and *reverberii* in *Telmatobius*.

Much of the confusion and debate surrounding the generic placement of these species stems from the limited morphological data. In an attempt to resolve the issues I studied examples of all seven species. The following descriptions include primarily osteological data; brief synopses of soft anatomies are appended. Taxonomic conclusions are deferred to a section following the account of morphology. *Telmatobius grandisonae* is imperfectly known; the following account does not pertain to *T. grandisonae*.

## Morphology

*Cranial skeleton*.—In all species the frontoparietals are paired and of limited extent, exposing a large frontoparietal fontanelle. The fontanelle is least extensive in *nitoides* and *somuncurensis*. The frontoparietals rest on the posterior edge of the sphenethmoid and do not contact the nasal bones. Posteriorly, the frontoparietals meet in *nitoides* and nearly do in *somuncurensis*. In all six species the frontoparietals extend laterally and posteriorly onto the otooccipitals, but in none of the species are the frontoparietals fused with the otooccipitals. The frontoparietals are not ornamented, nor is there any trace of supraorbital flange or crest formation.

The nasal bones are comparatively large elements in *nitoides*, *patagonicus*, *praebasalticus*, *reverberii*, and *solitarius*, but are smaller in *somuncurensis* (Fig. 2). In all of these frogs the nasals are narrowly separated or in tenuous contact. Laterally, the nasals are narrowly separated from the *pars facialis* of the maxilla except in *somuncurensis* (in contact).

The maxillary arch is incomplete in all six species. The deleted element is the quadratojugal. The alary processes of the premaxillae are directed dorsally or somewhat anterodorsally in all species except *somuncurensis* in which they are directed posterodorsally (Fig. 2). The *pars dentalis* bears pedicellate teeth in all species. Gallardo (1962) originally described *patagonicus* as a *Batrachophrynus*. This species differs from the other Patagonian species in having weakly ankylosed teeth on the premaxillae, maxillae, and prevomers but is never completely edentate. In seven juvenile *patagonicus*, the

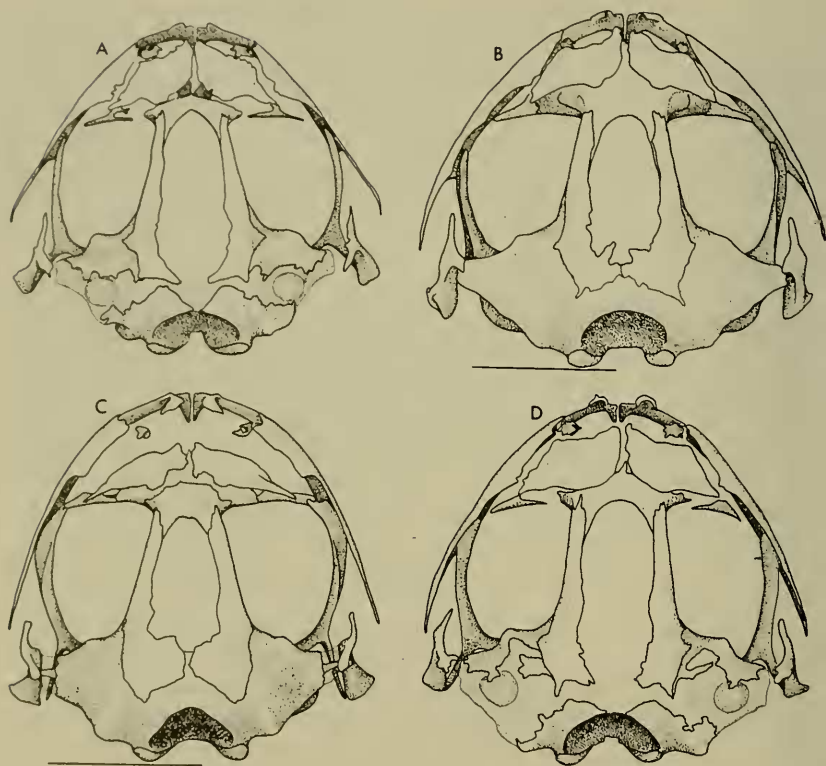


FIG. 2.—Dorsal views of skulls of Patagonian “*Telmatobius*.” (A) *solitarius* (IBA-UNC uncatalogued 5A), (B) *nitoi* (CHINM 6875), (C) *somuncurensis* (IBA-UNC 2135/8), and (D) *patagonicus* (IBA-UNC uncatalogued 2A). Line equals 5 mm.

number of premaxillary teeth varies from 3–6 ( $\bar{x} = 4.50$ , 2 SE = 0.50, N = 14) per premaxilla. The number of teeth per maxilla in these 7 individuals varies from 0–7 ( $\bar{x} = 2.93$ , 2 SE = 1.14, N = 14). The prevomers have 0–1 teeth per odontophore ( $\bar{x} = 0.43$ , 2 SE = 0.27, N = 14). In 11 adults, the number of teeth per maxilla ranges from 3–16 ( $\bar{x} = 10.14$ , 2 SE = 1.55, N = 22); the number of teeth per premaxilla ranges from 4–10 ( $\bar{x} = 7.09$ , 2 SE = 0.64, N = 22); and the number of teeth per prevomerine odontophore varies from 0–2 ( $\bar{x} = 1.27$ , 2 SE = 0.27, N = 22). The palatine process is prominent and easily distinguished from the *pars palatina*, which is narrow in each of the species but broadens slightly near the point of articulation with the maxilla. The premaxillae are relatively narrow (as in most advanced frogs)—the maxilla length/premaxilla width ranges from 3.5 (*reverberii*, *solitarius*, *somuncurensis*) to 5.0 (aquatic *patagonicus*).

The maxillae bear teeth in all but some young specimens of *patagonicus*. The *pars facialis* bears a prominent preorbital process but below and posterior to the orbit the *pars facialis* is insignificant. The *pars palatina* is narrow through the length of the maxilla although it narrows more markedly posterior to the pterygoid-maxilla articulation. No pterygoid process is developed.

The parasphenoid is triradiate in all six species and the cultriform process extends anteriorly to just posterior to the level of the palatines in *nitoides*, *patagonicus*, *solitarius*, and *somuncurensis* but extends more anterad (just anterior to level of the palatines) in *praebasalticus* and *reverberii*. The parasphenoid alae are oriented at right angles to the cultriform process (or feebly deflected posteriorly). No odontoids or ridges appear on the ventral surface of the bone.

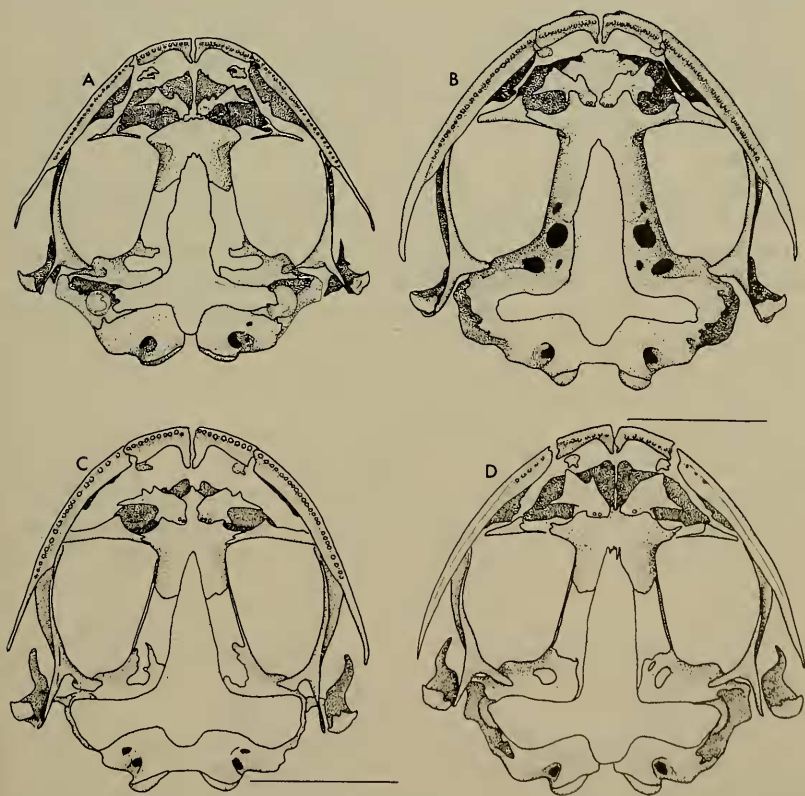


FIG. 3.—Ventral views of skulls of Patagonian “*Telmatobius*.” (A) *solitarius* (IBA-UNC uncatalogued 5A), (B) *nitoides* (CHINM 6875), (C) *somuncurensis* (IBA-UNC 2135/8), and (D) *patagonicus* (IBA-UNC uncatalogued 1A). Line equals 5 mm.

The prevomers are entire in each of the Patagonian *Telmatobius* but are relatively small bones. The dentigerous processes are usually present (except in small individuals) and bear teeth. The processes are situated between the choanae. The prevomers do not contact any of the other dermal bones of the skull. The palatines are uniformly present but are small, not contacting the maxillae or the sphenethmoid except in *somuncurensis* (Fig. 3). In all of the species there is an anterior flange on the palatines—these are best developed in *nitoid* and *solitarius*.

The triradiate pterygoids are relatively small. The anterior ramus articulates with the maxilla in an articulation extending nearly to the planum antorbitale (*patagonicus*, *somuncurensis*) or is only briefly in contact with the maxilla (*nitoid*, *solitarius*). The median ramus is reduced in all of these frogs and does not bear a bony articulation with the otic capsule in *nitoid*, *reverberii*, and *solitarius*; the median ramus is larger and does contact the otic capsule in *patagonicus*, *praebasalticus*, and *somuncurensis*.

The zygomatic rami of the squamosals are present and moderately long. The otic rami are small and directed medially toward the cristae paroticae but do not articulate or overlap the cristae paroticae.

The septomaxillae are uniformly present and proportionately large in each of these species; the elements are least large in *somuncurensis*. The sphenethmoid is weakly ossified in five species but is extensive in *nitoid* (extending anteriorly to near the anterior edge of the nasals and posteriorly to enclose the optic foramen). In the other species, the ossification extends to beneath the posterior edge of the nasals (*patagonicus*, *solitarius*) or fails to reach the nasals (other three species).

The otooccipital is weakly ossified in all species except *nitoid* and the prootic and exoccipital are clearly defined. The epiotic eminences are relatively low and the crista parotica is best described as short and stocky. An operculum is evident in each of the species but the pleetrum (columella) is present only in *somuncurensis*. (The cavum tympanicum and tympanic annulus are likewise absent in *nitoid*, *patagonicus*, *praebasalticus*, *reverberii*, and *solitarius*; these features are present in *somuncurensis*). The occipital condyles are not stalked and are not confluent. The condyles are slightly separated in all species except in *nitoid* (Fig. 2-3).

*Postcranial axial skeleton*.—All six species are uniformly procoelous and have 8 presacral vertebrae; the cervical and second vertebra are not fused. The cotylar facets of the atlas are broadly to narrowly separated. Few specimens exhibit the clearly type II atlantal condition previously reported for *Telmatobius* (Lynch, 1971). Only *solitarius* and *somuncurensis* exhibit the type II (closely

juxtaposed cotyles) atlantal condition. The other four species have more widely separated cotyles approaching a type I condition. I am reluctant to term the atlases of these four species as type I. The neural arches are not imbricate (Fig. 4), although the exposure of the nerve canal varies concordantly with general levels of ossification (least non-imbricate in *nitoi* and *solitarius*—most non-imbricate in *patagonicus* and *reverberii*). The neural arches lack crests. Vertebrae II through IX (sacrum) bear transverse processes and lack ribs (even in the newly metamorphosed individuals). With the exception of *reverberii* (see below), the transverse processes are prominent on vertebrae II–VIII. Those of vertebrae II–IV are perceptibly broader than those of vertebrae V–VIII. The transverse processes are deflected anteriorly on vertebrae II, III, VII, VIII, and sometimes VI, and are deflected posteriorly on vertebrae IV, V, and sometimes VI. Those of VI are oriented anteriad in *nitoi* and *patagonicus* but posteriorly in *praebasalticus*, *solitarius*, and *somuncurensis*.

The widths of the transverse processes (measured from the tip of the process to the base of the prezygapophysis along the anterior edge of the process) are in order of decreasing length—III, II and IV, V, VI, VII, VIII. In *patagonicus*, the transverse processes of vertebrae II–IV are broader than or as broad as the sacral diapophyses (98–118%). The processes of vertebrae V–VIII are much narrower than the sacral diapophyses (49–68%). The transverse processes of vertebra III are broader than the sacral diapophyses in *praebasalticus* and *somuncurensis* but not in *nitoi* or *solitarius* (Fig. 5). In these last two species the processes on II–IV are

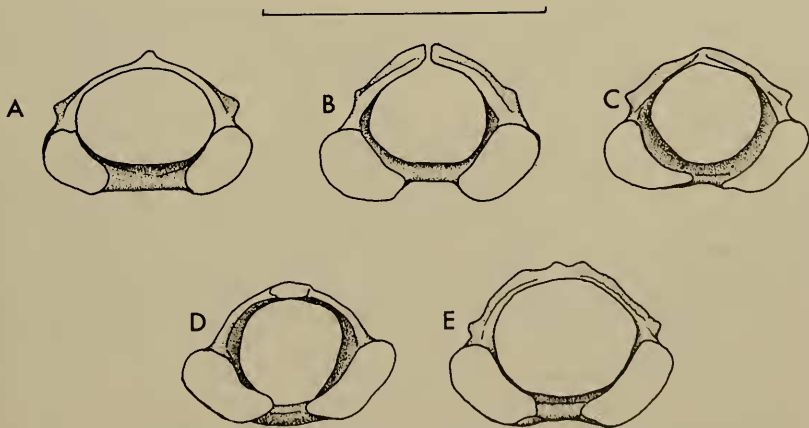


FIG. 4.—Anterior views of atlases of Patagonian “*Telmatobius*.” (A) *nitoi* (CHINM 6875), (B) *patagonicus* (IBA-UNC uncatalogued 1A), (C) *solitarius* (IBA-UNC uncatalogued 5A), (4) *somuncurensis* (IBA-UNC 2135/8), and (E) *Alsodes gargola* (CHINM 7082). Line equals 5 mm.

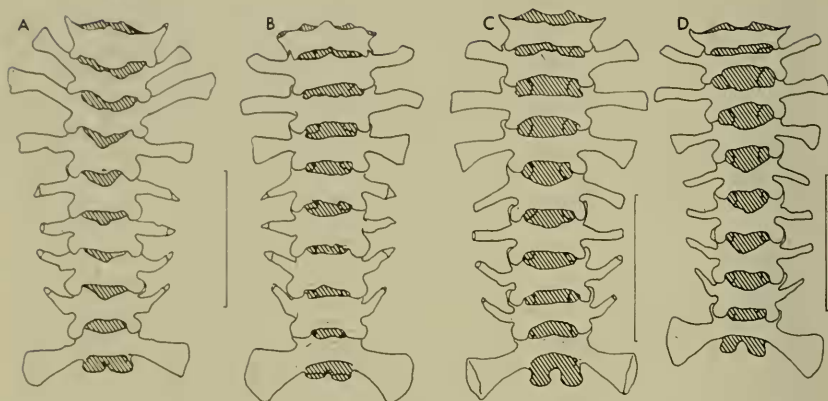


FIG. 5.—Dorsal views of vertebral columns of Patagonian “*Telmatobius*.” (A) *somuncurensis* (IBA-UNC 2135/8), (B) *nitoi* (CHINM 6875), (C) *patagonicus* (IBA-UNC uncatalogued 1E), and (D) *solitarius* (IBA-UNC uncatalogued 5A). Lines equal 5 mm (scale between A and B applies to both).

broader than the processes on V–VIII. The same situation is the case in *praebasalticus*. In *somuncurensis*, the processes of vertebrae II, III, and IV are subequal in width and not strikingly broader than the processes of vertebra VI.

The sacral diapophyses are deflected posteriorly in each species. The diapophyses are most dilated (ratio of length to width) in *nitoi* (0.96) and *patagonicus* (0.84), but are much less dilated in *praebasalticus* (0.64), *solitarius* (0.71), and *somuncurensis* (0.54). In no case could the diapophyses be described as “expanded or dilated” (and thus equivalent to the character state seen in many bufonids), but they are more dilated than is the case in most telmatobine frogs.

In terms of vertebral morphology, *reverberii* is the most distinctive of the Patagonian *Telmatobius*. The transverse processes of vertebrae V–VIII are extremely short. The deflection of the processes of the posterior vertebrae cannot be satisfactorily described but the deflection of the anterior vertebrae (II–IV) conforms with that seen in the other Patagonian species. The transverse processes of vertebrae II–IV are broader than the sacral diapophyses (103–147%). The sacral diapophyses are not dilated but are weakly deflected posteriorly. The centra are proportionately very broad (compare Fig. 6 A and D) when compared with those of adults of the other five Patagonian *Telmatobius*. The skeletons of *reverberii* available to me include a number of juveniles; the largest specimens are not mature (26.5–27.5 mm SVL contrasting with adult size range of 35–38 mm given by Cei, 1969a). Comparing the skeletons of the



largest *reverberii* available to me with those of immature *patagonicus* (Fig. 6 C) prompts the conclusion that the broad centra of my *reverberii* are reflections of immaturity. The failure of the centra of the anteriormost vertebrae to ankylose with the neural arches is also a reflection of immaturity. The lack of sacral diapophyseal dilation may also be due to age but the brevity of the transverse processes of the posterior vertebrae in *reverberii* appears not to be due to age. The centra appear to be stegochordal but my preparations do not permit a definitive statement.

The ilial shaft is elongate bearing little or no dorsal crest (Fig. 7). The dorsal prominence is small, conical, and directed dorso-laterally (a protuberance is not clearly evident). The dorsal acetabular expansion is small with little dorsal vector. The ventral acetabular expansion is moderate-sized. The angle of ventral acetabular expansion is about 90°. The acetabulum is large and weakly emarginate dorsally. The preacetabular zone is broad. The ischium is small and lacks prominent processes. The pubis is small and cartilaginous.

The hindlimb skeleton is not noteworthy. The femur and tibio-fibula lack processes or hooks. The tibulare and fibulare are not fused. Two tarsalia are present. The metatarsals and phalanges are not modified, and the primitive phalangeal formula (2-2-3-4-3)

The sacrococcygeal articulation is bicondylar in all six species. The coccyx does not bear transverse processes or prezygapophyses. It is unmodified. The terminal phalanges are knobbed. If a prehallux

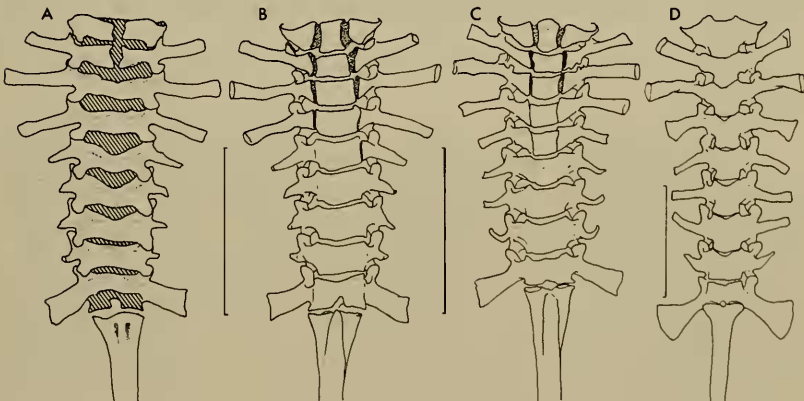


FIG. 6.—Vertebral columns of Patagonian “*Telmatobius*.” (A and B) dorsal and ventral views, *reverberii* (IBA-UNC uncatalogued 4A); ventral views of that of a (C) juvenile *patagonicus* (IBA-UNC uncatalogued 2C) and (D) an adult *patagonicus* (IBA-UNC uncatalogued 1A). Scale for A and B between them; lines equal 5 mm.

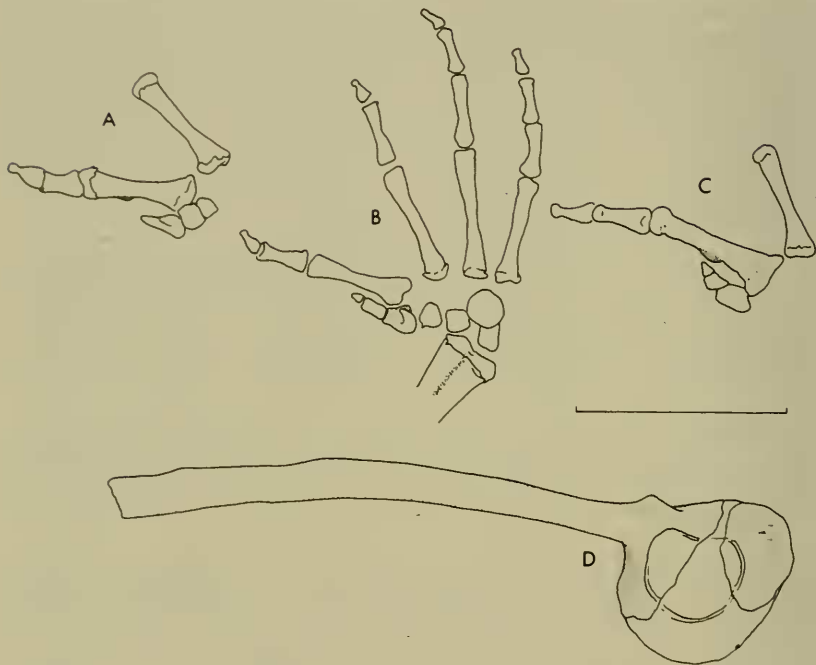


FIG. 7.—(A) prepollex, thumb, and second metacarpal of left hand of *nitou* (male, CHINM 6875), (B) palmar view of hand of *patagonicus* (male, IBA-UNC uncatalogued 3A), (C) prepollex, thumb, and second metacarpal of left hand of *somuncurensis* (male, IBA-UNC 2135/8), and (D) pelvis of *patagonicus* (IBA-UNC uncatalogued 1E). Line equals 5 mm.

is present, the element is cartilaginous and does not pick up Alizarin stain.

*Pectoral girdle and appendages.*—The pectoral girdles of all six species are arciferal. Procoracoid cartilages are present extending laterally along  $\frac{2}{3}$  to  $\frac{3}{4}$  the width of the clavicles. The procoracoids are fused anteromedially in *patagonicus* but are free in *somuncurensis*. The epicoracoidal cartilages are free for their entire lengths (except at the procoracoid or procoracoid bridge) and end posteriorly as prominent epicoracoidal horns lateral to the sternum. The omosternum is uniformly present. It is narrow and elongate in all species except *somuncurensis* in which it broadens anteriorly (Fig. 8). I found no omosternal ossifications.

The clavicles are strongly arched (tips extending anterior to a line between the anterior edges of the scapulae) and in contact medially. The posterior border (on the medial  $\frac{2}{3}$ ) bears a thin flange which increases the length of the bone (this is simply ossification of

the procoracoidal cartilages). The clavicle does not overlay the *pars acromialis* of the scapula. Clavicle width/scapula width is 0.95–1.2 in the six species. The scapula is proximally bicapitate. The coracoids are narrowly dilated at their distal and proximal ends, narrower than the clavicles, and somewhat thicker elements than the clavicles.

The sternum is longer than broad in all six species. In all but *somuncurensis*, the sternum is plate-like, weakly expanded posterolaterally, weakly pointed posteriorly, and lacks internal ossification (Fig. 8). In *somuncurensis*, the sternum is deeply incised posteriorly (for about one-half its length) and somewhat expanded posterolaterally. Anterior to the incision are two rectangular ossifications.

The skeleton of the forelimb is not noteworthy. The humerus bears a normal-sized *crista ventralis* (*deltoidea*), a narrow *crista lateralis*, and a slightly larger *crista medialis*. On the humeri of *nitoidi*, the *spina tuberculum medialis* is visible (Fig. 9). The forelimbs of the males of these species are not massive when compared to those of females, and that is reflected in the modest development of humeral crests. The phalangeal formulae for the manus is the primitive condition (2–2–3–3), and the terminal phalanges are knobbed. The prepollex consists of three elements and is small (less than half the length of the first metacarpal). The inner metacarpal of males of *nitoidi* and *somuncurensis* bears a short flange at the midpoint of the medial margin of the bone (Fig. 7). This condition is not seen in *patagonicus*, *praebasalticus*, or *solitarius*. I do not have adult males of *reverberii*.

*Secondary sex characteristics*.—Males of each of the six species have nuptial pads on the thumb. In some species the excrescences

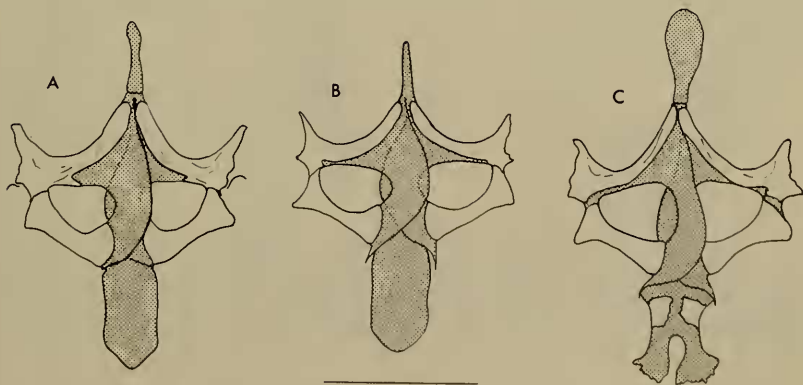


FIG. 8.—Ventral views of pectoral girdles (excluding scapulae, supra-scapulae, and cleithra) of (A) *nitoidi* (CHINM 6875), (B) *patagonicus* (IBA-UNC uncatalogued 3A), and (C) *somuncurensis* (IBA-UNC 2135/7). Line equals 5 mm. Cartilage is stippled.

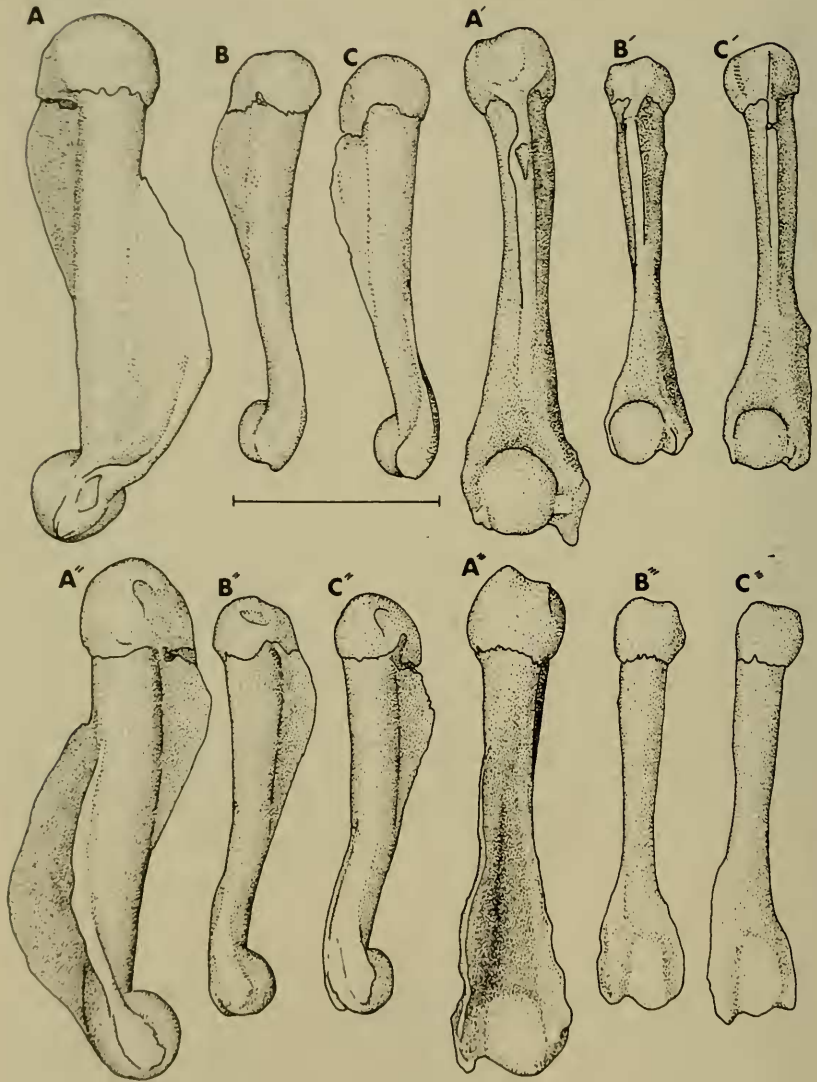


FIG. 9.—Right humeri of male Patagonian "Telmatobius"; medial, anterior, lateral, and posterior views, respectively, of *Alsodes gargola* (A, A', A'', A'''; CHINM 7082), *Atelognathus nitoi* (B, B', B'', B'''; CHINM 6875), and *Somuncuria somuncurensis* (C, C', C'', C'''; IBA-UNC 2135/8). Line equals 5 mm.

extend onto the second and even third fingers. In every case the nuptial spines are small, close-set, and numerous, forming a roughened pad. None of the six species shows any trace of nuptial armament on the chest, and all species appear to lack spicules on the

skin of the dorsum and hind legs. As mentioned above, the forearms of the male are not greatly enlarged.

On the basis of data provided by Cei (1969a, 1970a, 1972), Barrio (1973), and Cei and Roig (1968), there seems to be no appreciable size difference between males and females. Vocal sacs and slits are absent in all species.

*Other traits.*—The tympanic annulus is visible only in *somuncurensis*; this structure as well as the cavum tympanicum and plectrum is lost in the other five species. The pupil is a horizontal slit in each of the six species. The meniscus noted by Cei (1969a, 1972) in *somuncurensis* is not found in the other five species. The thumb is slightly longer than the second finger. The skin of the dorsum is smooth or weakly granular in the six species and not provided with obvious parotid, lumbar, or inguinal glands. This skin of the venter is smooth. The peculiar cloaca of *somuncurensis* (see Cei, 1969a, for illustrations) is unique. Tarsal folds occur in five species but are absent in *somuncurensis*. The folds are weakly developed and narrow in *praebasalticus*, but prominent in *nitoid*, *patagonicus*, *reverberii*, and *solitarius*. Two metatarsal tubercles, the inner larger than the outer and neither spade-like, occur in each of the six species. Considerable variation is exhibited in toe webbing. The toes of *nitoid* and *patagonicus* are fully webbed although the litoral populations of *patagonicus* have one phalanx of the fourth toe free of webbing. Two to two and one-half phalanges of the fourth toe are free of webbing in *praebasalticus* and *reverberii* (these species may be described as having the foot "half-webbed"). Three phalanges are free (one-third webbed) in *somuncurensis* and three and one-half (one-fourth webbed) in *solitarius*.

The posterior edge of the tongue is free (non-adherent to floor of mouth) and not notched in any of the species. Prevomerine odontophores are usually visible (if not visible, palpable) and are situated between the moderate-sized choanae.

Karyotype data are available for five of the species. Four have diploid counts of 26 chromosomes (Barrio, 1973, Barrio and Rinaldi de Chieri, 1970, Cei, 1969b)—*nitoid*, *patagonicus*, *praebasalticus*, and *reverberii*. Barrio (1973) reported a secondary constriction on chromosome 6. The karyotypes of *nitoid*, *patagonicus*, and *praebasalticus* consist of five pairs of large chromosomes and eight pairs of small chromosomes. Cei (1969b:269) mentioned that *somuncurensis* has a 2N of 22.

#### Taxonomic Conclusions

The morphology of the Patagonian "*Telmatobius*" provides support for the following taxonomic conclusions:

1) Gallardo's (1962, 1970) assignment of *patagonicus* to *Batrachophrynus* cannot be supported because *patagonicus* has teeth on the maxillary arch and prevomer (*Batrachophrynus* is edentate), and *patagonicus* has a narrow *pars palatina* of the premaxilla and lacks a quadratojugal. In *patagonicus* the transverse processes of the posterior presacral vertebrae are shortened and the sacral diapophyses are weakly dilated. The tongue is present and its posterior edge is free in *patagonicus*, unlike the condition in the two species of *Batrachophrynus*. The similarity of *patagonicus* to *Batrachophrynus* is best viewed as convergence through adaptation to similar habitats.

2) Gallardo's (1970) assignment of *praebasalticus* and *reverberii* to *Alsodes* is rejected on two bases. Firstly, neither species exhibits the greatly enlarged forearm (and humeral spines or flanges) purportedly characteristic of males of *Alsodes*; neither species has nuptial armature on the chest of the male, and neither species exhibits the expanded and posteriorly notched sternum characteristic of *Alsodes* (Gallardo, 1970). Secondly, these species share a number of character states of skeletal features with *nitoi*, *patagonicus*, and *solitarius* (*viz.*, lack of quadratojugal, very large frontoparietal fontanelles, and relatively large juxtaposed nasals) in contrast to the character-states for the same characteristics in the other species usually assigned to *Alsodes* (*gargola*, *montanus*, *monticola*, and *nodosus*).

3) The six species are not members of *Telmatobius*. Unlike *Telmatobius*, the Patagonian species lack quadratojugal bones. Loss of the quadratojugal is rare among leptodaetyloid frogs—only seven other leptodactyloid genera exhibit the loss (the Cycloranine *Notaden*, the Elosiine *Crossodactylus*, the Leptodaetylines *Pleurodema* and *Pseudopaludicola*, and three Telmatobiines, *Batrachyla*, *Hylorina*, and *Insuetophrynus*).

4) One of the Patagonian species, *somuncurensis*, exhibits a low character-state congruence with the other five. Unlike those species, *somuncurensis* has moderate-sized, medially separated, ellipsoid nasal bones, contact between the maxilla and nasal, posterodorsally directed alary processes of the premaxillae, fully developed ears, a large, spatulate omosternum, a deeply notched (bifurcate) sternum bearing a pair of endochondral ossifications, 11 pairs of chromosomes, and lacks a tarsal fold. One other trait of *somuncurensis*, unusual among Neotropical leptodaetyloids, is inguinal amplexus (Cei 1972; 447, fig. 5).

The architecture of the skull, vertebral column, and pectoral girdle of *somuncurensis* are similar to the conditions seen in the leptodactyline genus *Pleurodema*. The chromosome number for *somuncurensis* ( $2N = 22$ ) agrees with the modal count for the

Leptodactylinae rather than that for the lower telmatobiines (2N = 26). Although the sternal condition in *somuncurensis* approaches the condition seen in several *Pleurodema*, no sternal style is developed. The type II cervical cotylar arrangement in *somuncurensis* is unlike the type I arrangement found in *Pleurodema* and the other leptodactylines. The occurrence of inguinal amplexus is unusual among Neotropical leptodactylids but is duplicated in *Pleurodema bufonina* and the bufonids of the genus *Osornophryne*.

The low character-state congruence between *somuncurensis* and the other Patagonian *Telmatobius* coupled with a number of similarities between the seven species and between *somuncurensis* and the leptodactylines of the genus *Pleurodema* suggest that *somuncurensis* should be placed in its own genus and viewed as annectant between the Patagonian *Telmatobius* and *Pleurodema*.

5) The remaining Patagonian species cannot be placed in any currently recognized genus of the Leptodactylidae. The architecture of the pectoral girdle, skull, and vertebral column, as well as the simple digits (no dermal scutes, no discs or pads), and presence of aquatic larvae in the life cycle support assignment to the Telmatobiinae. Within the Telmatobiinae, the Grypiscini and Eleutherodactylini exhibit more advanced and/or specialized features than seen in the Patagonian species (Lynch, 1971). The Odontophrynini have a ceratophryne-type ilium and markedly differ in the arrangement of skull bones and in pectoral architecture (Lynch, 1971). The Patagonian species do exhibit resemblances to those telmatobiines placed in the tribes Alsodini, Batrachyliini, and Telmatobiini. These three putative tribes include the following genera (not all previously recognized by all authors): *Alsodes*, *Batrachophrynus*, *Batrachyla*, *Caudiverbera*, *Eupsophus*, *Hylorina*, *Insuetophrynus*, *Telmatobufo*, *Telmatobius*, and *Thoropa*. Barrio and Rinaldi de Chieri (1971) suggested that *Limnomedusa* (placed in the Leptodactylinae by Lynch, 1971) also belongs with this assemblage.

#### *Atelognathus* new genus

*Type species.*—*Batrachophrynus patagonicus* Gallardo, 1962.

*Diagnosis.*—A genus of Telmatobiine Leptodactylids unique in having large, frontoparietal fontanelles, short palatine bones (not contacting the maxilla or calcified sphenethmoid), large nasal bones in median contact, lacking quadratojugals, plectra (columellae), tympanic annuli, and cavi tympani. The pectoral girdle is arciferal with an elongate, non-spatulate omosternum, and non-bifurcated sternum lacking endochondral ossifications. The cervical cotylar arrangement is type II or intermediate between types I (concave) and II (convex). The eight procoelous presacral vertebrae are independent and lack a vertebral shield. The transverse processes of presacral vertebrae V–VIII are short. The sacral diapophyses are

weakly dilated. The ilium is of the leptodactyline type. Terminal phalanges knobbed. Tadpoles with  $\frac{2}{3}$  tooth rows, labial papillae interrupted anteriorly, pond type.

*Etymology*.—Greek, *atelēs* and *gnathos*, meaning incomplete jaw; in reference to the lack of a quadratojugal in the maxillary arch.

*Content*.—Six species: *A. grandisonae* (Lynch), *A. nitoi* (Barrio), *A. patagonicus* (Gallardo), *A. praebasalticus* (Cei and Roig), *A. reverberii* (Cei), and *A. solitarius* (Cei).

*Remarks*.—*Atelognathus* is readily associated with the ten genera listed above. In the lack of quadratojugals, *Atelognathus* resembles *Batrachyla*, *Hylorina*, and *Insuetophrynus*. The three genera differ from *Atelognathus* in having small, medially separated nasal bones, long palatine bones (resting against calcified sphenethmoid and maxilla), and in having complete ears. *Batrachyla* differs further in having T-shaped terminal phalanges, the first finger shorter than the second, and the larvae have a complete series of papillae about the mouth. *Hylorina* has greatly elongated digits, vertical pupils, and the larvae have 2/2 tooth rows. *Insuetophrynus* has large spines on the thumb and chest of the reproductively active male and has a very narrow frontoparietal fontanelle.

*Atelognathus grandisonae* is the most southern species of the genus. It differs from the other five species in having a dilated manubrial portion of the omosternum, narrowly separated nasal bones, and complete coverage of the frontoparietal fontanelle. More material is required to verify the generic assignment; perhaps the most critical datum is the breadth of the palatine bones.

### Somuncuria new genus

*Type-species*.—*Telmatobius somuncurensis* Cei, 1969.

*Diagnosis*.—A genus of telmatobiine leptodactylids unique in having a large frontoparietal fontanelle, long palatine bones, moderate-sized nasal bones, plectra, cavi tympani, and tympanic annuli, and in lacking quadratojugal bones. The pectoral girdle is arciferal with an elongate, spatulate omosternum, and the sternum is bifurcated and bears two endochondral ossifications. The cervical cotylar arrangement is type II. The eight procoelous presacral vertebrae are independent and lack a vertebral shield. The transverse processes of presacral vertebrae V–VIII are short and the sacral diapophyses very slightly dilated. The ilium is of the leptodactyline type. Terminal phalanges are knobbed. Tadpoles with  $\frac{2}{3}$  tooth rows, labial papillae interrupted anteriorly, pond type. Amplexus inguinal.

*Etymology*.—The generic name is taken from the name of the isolated Patagonian plateau on which the frog lives.

*Content*.—*Somuncuria somuncurensis* (Cei); monotypic.

*Remarks*.—*Somuncuria somuncurensis* is intermediate between



the Patagonian genus *Atelognathus* (Telmatobiinae) and the leptodactyline genus *Pleurodema* and is conceivably a survivor of a transitional stage in the early evolution of the Leptodactylinae from the Telmatobiinae. *Somuncuria* resembles *Pleurodema* in the arrangement of skull bones, its karyotype, and in having a sternum approaching the styler condition seen in leptodactylines.

In habitus, *S. somuncurensis* is quite similar to some *Atelognathus* and *Telmatobius* and rather unlike any *Pleurodema* or other leptodactyline. It differs from the other lower telmatobiines having lost the quadratojugals in the same ways they differ from *Atelognathus* (see above) and differs from *Atelognathus* in having broad palatines, a protruding cloaca (Cei, 1969a), and inguinal amplexus.

#### THE LOWER TELMATOBIINES

Lynch (1971) recognized 25 genera in the leptodactylid subfamily Telmatobiinae and divided the subfamily into five tribes (Alsodini, Eleutherodactylini, Grypiscini, Odontophrynini, and Telmatobiini). Subsequently (Lynch, 1973), the Alsodini was partitioned into the Alsodini and Batrachylini. The tribes Alsodini, Batrachylini, and Telmatobiini are collectively termed the lower telmatobiines. Twelve genera make up the lower telmatobiines: *Alsodes*, *Atelognathus*, *Batrachophrynus*, *Batrachyla*, *Caudiverbera*, *Eupsophus*, *Hylorina*, *Insuetophrynus*, *Somuncuria*, *Telmatobius*, *Telmatobufo*, and *Thoropa*. Most are rare and accordingly morphological and biological data are scarce. A number of them are illustrated in Fig. 10.

Heyer (1975) recognized "the telmatobines," an informal grouping including *Batrachophrynus*, *Batrachyla*, *Caudiverbera*, *Eupsophus*, *Hylorina*, *Insuetophrynus*, *Telmatobius*, and *Telmatobufo*. He placed *Thoropa* in an ecological assemblage containing elosines and grypiscines as well.

In the past five years I have been able to study skeletons of *Insuetophrynus* and *Telmatobufo* as well as those of *Alsodes gargola*, *A. montanus*, *Atelognathus*, *Batrachophrynus brachydactylus*, *Somuncuria*, and several species of *Telmatobius*. The data derived from study of these critical taxa require a re-interpretation of the relationships of the lower telmatobiines and allow some conclusions not previously possible. Morphological data for these lower telmatobiines follow:

#### *Alsodes gargola* Gallardo and *A. montanus* (Lataste)

*Skull*.—The frontoparietals are paired, not fused to the prootics, and moderately extensive exposing a frontoparietal fontanelle (Fig. 11). The fontanelle is narrower than that seen in most species of *Atelognathus* but more extensive than that illustrated in *Telma-*

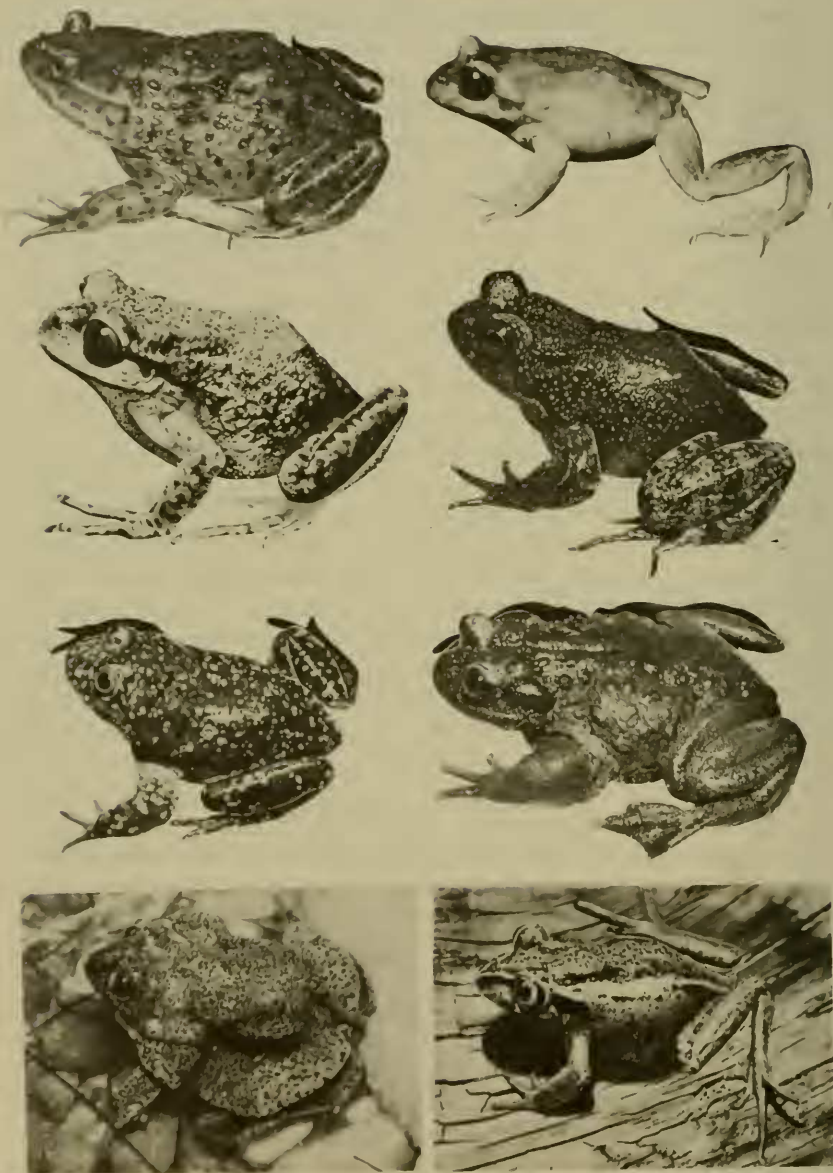


FIG. 10.—Representative tematobiine frogs: From left to right and top to bottom: *Atelognathus patagonicus*, KU 160427, ♂, 44.5 mm; *Batrachyla taeniata*, KU 161457, ♂, 30.0 mm; *Caudiverbera caudiverbera*, KU 161411, ♀, 106.5 mm; *Eupsophus vertebralis*, KU 162236, ♂, 49.4 mm; *Hylorina sylvatica*, KU 161391, ♀, 61.7 mm; *Insuctophrynus acarpicus*, KU 161413, ♂, 46.9 mm; *Telmatobius peruvianus*, KU 162058, ♂, 53.5 mm; *Telmatobufo venustus*, KU 161438, ♂, 75.6 mm. Photographs by William E. Duellman.

*tobius hauthali* or *T. marmoratus* by Lynch (1971). Anteriorly, the frontoparietals broadly rest on the posterolateral margins of the sphenethmoid. Posteriorly, the elements rest on the otoccipitals. The sphenethmoid is moderate-sized and the nasals rest on the anterolateral margins of the calcified portions of the element. The nasals are broadly separated from one another and from the frontoparietals; they bear long maxillary processes which nearly reach the maxillae. The nasals are relatively short and teardrop-shaped.

The maxillary arch is complete but less massive than that of *Telmatobufo venustus*. The premaxillae are relatively narrow and bear alary processes of moderate length directed dorsally. The 11-14 premaxillary teeth are moderately long, pedicellate, and well-ankylosed to the jaw. The *pars palatina* is narrow except where the moderate-length palatine processes are found. The *pars facialis* of the maxilla is relatively deep and restricted to the snout. The maxilla bears about 30 well-ankylosed teeth in a row extending to a point just posterior to the maxillopterygoid junction. The *pars palatina* is narrow and narrows abruptly at the posterior end of the maxil-

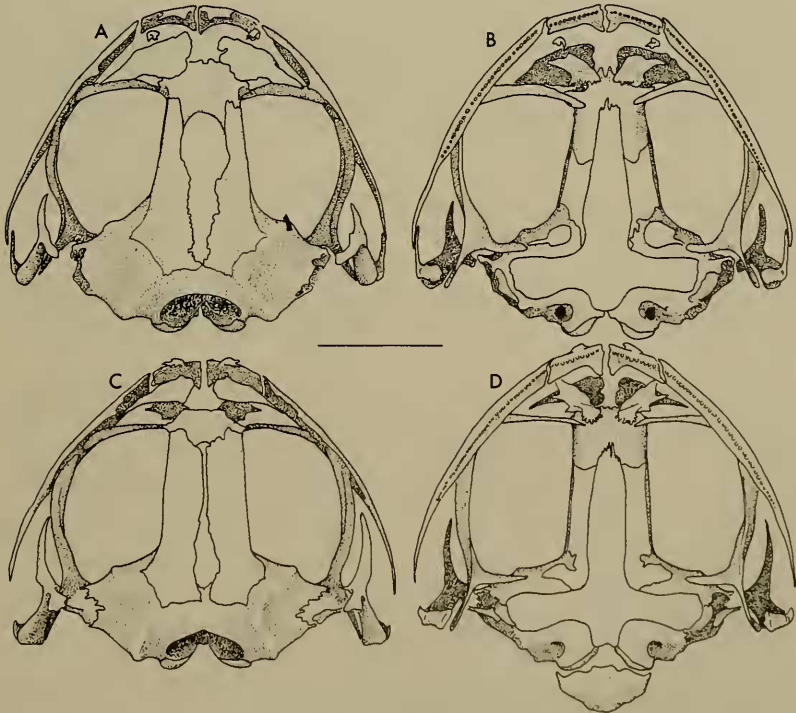


FIG. 11.—Skulls of (A) *Alsodes gargola* (CHINM 7082) and (B) *Insuetophrynus acarpicus* (CHINM 6903). Line equals 5 mm.

lopterygoid junction. No obvious pterygoid process is developed. The quadratojugal is of moderate-size and broadly articulates with the maxilla. The septomaxillae are small.

The otoccipital is well-ossified with low epiotic eminences. The cristae paroticae are short and stocky in *A. gargola* and slightly broader and narrower in *A. montanus*. Both have opercula and lack plectra. The occipital condyles are not stalked and are narrowly separated. The zygomatic ramus of the squamosal is of moderate length. The otic ramus is short. In *A. gargola* the otic ramus is directed medially and lacks an otic plate whereas in *A. montanus* it is not deflected medially but bears a small otic plate. In neither species does the otic ramus or plate contact the crista parotica.

The parasphenoid is cruciform. The cultriform process is long and gradually narrows anteriorly in *A. gargola*. The anterior end of the cultriform process extends to between the palatines in *A. gargola* but not as far anteriorly in *A. montanus*. The parasphenoid alae are oriented at right angles to the cultriform process in *A. gargola* but weakly deflected posteriorly in *A. montanus*. Both have a posterior ramus of the parasphenoid; the ramus is round posteriorly (not indented).

The pterygoids are relatively large. The anterior ramus rests on the palatal shelf of the maxilla but does not reach the palatines. The median ramus is of moderate length and abuts against the anterior face of the prootic overlapping the parasphenoid alae. The pterygoid does not bear a ventral flange.

The skull anterior to the palatines is not shortened. The palatines are broad and arched, extending from the maxillae to the sphenethmoid. The anterior flange is better developed in *A. montanus* but perceptible in *A. gargola*. The small prevomers lie well anteriorly to the palatines, are broadly separated, entire, and bear rows of 6-7 well-ankylosed teeth on prominent odontophores lying between the choanae.

*Postcranial skeleton.*—The vertebral column contains eight independent, prococlous, presacral vertebrae. The cervical cotyles are moderately separated. The neural arches are non-imbricate and lack crests. Vertebrae II-IX bear transverse processes and lack ribs. The transverse processes of II-IV are larger (thicker and wider) than those of V-VIII. In *gargola*, the processes of II, VI-VIII are deflected anteriorly and IV-V are deflected posteriorly. In *montanus*, the processes of II, VII-VIII are deflected anteriorly and III-VI deflected posteriorly. In order of decreasing widths, the transverse processes of *gargola* are III, IX, II, IV, V, VI-VIII; those of *montanus* are III, IV and IX, II, V, VI, VII, VIII. The sacral diapophyses are oriented at right angles to the sagittal plane or very weakly deflected posteriorly. The sacral diapophyses are weakly

dilated (L/W 0.82–0.90 in *gargola*; 0.77–0.82 in *montanus*). The sacrocoyceal articulation is bicondylar. The coccyx lacks lateral flanges and is not inflated anteriorly. In *A. montanus* there is a pair of thin processes arising on the arch (Fig. 12); these are not vertebral like structures. The ilium bears a very slight ridge-like dorsal crest; the dorsal prominence is the same as that in *Insuetophrynus*.

The clavicles are massive and curved. The omosternum is short and bears a manubrial dilation. The sternum broadens posteriorly, is weakly inflated posteriorly, and is feebly notched. The sternum bears an irregular-shaped endochondral ossification. The humerus in males bears enlarged *cristae medialis*, *lateralis*, and *ventralis* (Fig. 9).

**Batrachophrynus brachydactylus Peters**

The skeleton of a single specimen of this rare aquatic leptodactylid is available. The skull exhibits few departures from the description and illustration of *B. macrostomus* given by Lynch (1971). The nasals are shorter than in *macrostomus* but in that species are broadly in contact medially and extend laterally to form sutures with the *pars facialis* of the maxilla and anterior ramus of the pterygoid. In *B. brachydactylus*, the frontoparietals are separated for most of their length exposing a long, narrow fontanelle; the frontoparietals are in sutural contact posterior to the fontanelle. The cultriform process of the parasphenoid is shorter in *B. brachydactylus*, extending anteriorly to the level of the palatines. Unlike *B.*

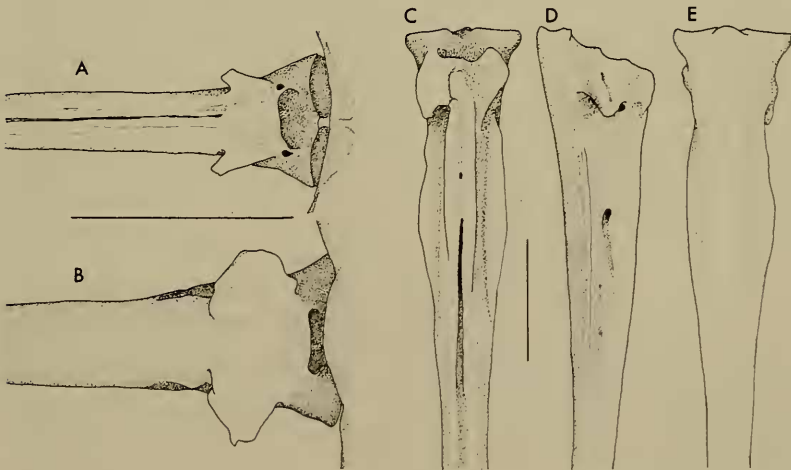


FIG. 12.—Coccyges of telmatobiines. (A) *Alsodes montanus* (IBA-UNC 1646/2), (B) *Telmatobufo venustus* (KU 159811) and (C) dorsal, (D) lateral, and (E) ventral views of *Batrachophrynus brachydactylus* (SDSNH 46894). Lines equal 5 mm.

*macrostomus*, *B. brachydactylus* has completely lost the prevomers. Both species are completely edentulous and both have broad *pars palatina* of the premaxilla and maxilla. The median ramus of the pterygoid articulates with the parasphenoid ala and rests on the prootic. A plectrum as well as opereulum is present in *B. brachydactylus*.

*Postcranial skeleton*.—As in *B. macrostomus*, there are eight procoelous persaeral vertebrae. The cervical and second vertebrae are not fused. The cervical cotyles are narrowly separated. The neural arches are imbricate on anterior vertebrae but non-imbricate on posterior vertebrae; the arches lack crests. Vertebrae II–IX bear transverse processes without ribs. The transverse processes of vertebra II are narrower than those of III–IX (subequal in width). The transverse processes of vertebrae III–VI and IX are deflected posteriorly, of II and VIII are deflected anteriorly, and of VII are perpendicular to the sagittal plane. The sacral diapophyses are not dilated (L/W 0.58–0.60). The sacrococcygeal articulation is bicondylar. The coccyx bears flanges along the anterior one-third of its centrum (Fig. 12) similar to those seen in *Bufo blombergi*. The anterior end of the coccygeal neural arch is conspicuously inflated and posterolateral to the inflated arch are large spinal nerve foramina. More posteriorly one finds the smaller foramina normally seen on the coccyx. No prezygapophyses or transverse processes are borne on the coccyx (in *B. macrostomus* short transverse processes are found).

The pectoral girdle is short, broad, and areiferal. The omosternum is long and narrow and lacks a manubrial portion. The elavicles are massive and strongly curved; their massiveness is in part due to ossification of the procoracoidal cartilages posterior to the elavicles. The coracoids are less broad and less massive than the clavicles. The sternum is as long as broad (greatest breadth), gradually broadening posteriorly, is notched posteriorly, and bears a broad endochondral ossification. The humerus of males does not bear enlarged *cristae medialis* and *lateralis*.

#### *Insuetophrynus acarpicus* Barrio

*Skull*.—The frontoparietals are paired, not fused with the prootics, and extensive. A narrow frontoparietal fontanelle is exposed (Fig. 11). The frontoparietals rest on the posterior edge of the sphenethmoid and are broadly separated from the nasals. The nasal bones are broad and short, lie anterolateral to the calcified sphenethmoid, are broadly separated, and do not contact the maxillae.

The maxillary arch is incomplete; the quadratojugal is absent. The alary processes of the premaxillae are short and directed anterodorsally. The palatine process is short and broad. The *pars palatina*

is narrow except where it broadens into the palatine process. The premaxillae are relatively narrow. The maxillae bear 30-35 well-ankylosed teeth to a point posterior to the maxillopterygoid articulation. The *pars palatina* gradually narrows posterior to the maxillopterygoid articulation. No pterygoid process is developed.

The otoccipital is weakly ossified. The epiotic eminences are low and the crista parotica stocky. The plectrum and operculum are present. The occipital condyles are not stalked and separated medially. The zygomatic ramus of the squamosal is moderately long. The otic ramus is short and directed medially toward the crista parotica but does not overlap the crista parotica.

The parasphenoid is cruciform; the cultriform process is long and extends onto the sphenethmoid but does not reach the level of the palatines. The parasphenoid alae are feebly deflected posteriorly. The parasphenoid bears a short posterior ramus that is weakly emarginate.

The pterygoids are of moderate size. The anterior ramus rests on the maxilla and nearly meets the palatines. The median ramus is relatively long, articulates against the anterior side of the prootic. The pterygoid does not bear a ventral flange.

The portion of the skull anterior to the palatines is short compared to most frogs. The palatines are nearly straight, thin, and broad, resting on the maxilla and sphenethmoid. The palatines lack an anterior flange. The prevomers are moderately large, entire, well-separated, and bear prominent odontophores lying slightly posterior to the choanae. The odontophores bear 6-7 well-ankylosed teeth.

*Postcranial skeleton.*—The vertebral column consists of eight procoelous presacral vertebrae; the cervical and second vertebrae are not fused. The cotylar facets are moderately separated (type II). The neural arches are not imbricate (comparable to the state seen in *A. patagonicus*) and lack crests. Vertebrae II-IX bear transverse processes and lack ribs. The transverse processes are broadest on vertebrae II-V and narrow on vertebrae VI-VIII; the transverse processes are deflected anteriorly on vertebrae II, VII-VIII, slightly posteriorly on III, and not deflected on IV-VI. The width of the transverse processes are, in order of decreasing widths, IX, III, IV, II, V, and VI-VIII.

The sacral diapophyses are deflected posteriorly and are not dilated (L/W 0.48-0.57). The sacrococcygeal articulation is bi-condylar. The anterior end of the coccyx is not inflated and does not bear transverse processes or any other vertebra-like form.

The ilium lacks a crest. The dorsal prominence is elongate and about twice as large as that in *Atelognathus*.

The pectoral girdle is functionally firmisternal but has free epi-choracoid horns. The omosternum is relatively short and bears a

dilated manubrial portion. The sternum is small and not dilated posteriorly. The humerus bears a normal-sized *crista ventralis* and insignificant *cristae lateralis* and *medialis*.

### Telmatobius

My earlier account of *Telmatobius* (Lynch, 1971) included data for *T. marmoratus* and *T. schreiteri* (or *T. hauthali schreiteri*). In cranial morphology, *T. barrioi*, *T. culeus*, and *T. niger* agree in all respects with *T. marmoratus* and *T. hauthali*. The five species differ in vertebral morphology in that the transverse processes of the presacral vertebrae are quite broad in *T. culeus*, less so in *T. marmoratus*, and even less so in *T. barrioi*, *T. niger*, and *T. hauthali* (Fig. 13). The intrageneric variation seen in this characteristic renders the characteristic of little or no value in inferring relationships. The sacral diapophyses are very slightly dilated (L/W values are 0.56–0.64 for *culeus*, 0.56–0.59 for *marmoratus*, 0.56–0.65 for *niger*, and 0.65 for *hauthali*).

Comparing the pectoral girdles of some additional species to my illustration (Lynch, 1971: 60, fig. 34B), *T. barrioi* and *T. marmoratus* have even less inflation of the omosternum (in each it narrows anteriorly) whereas *T. brevipes*, *T. culeus*, and *T. niger* have a slightly greater inflation than that illustrated, and *T. sanborni* has considerably greater inflation of an elongate omosternum. All seven species have the same sternal form except that the posterior notch is generally less pronounced.

The humerus bears enlarged crests in *T. barrioi*, *T. marmoratus*, and *T. hauthali*, but not in *T. brevipes*, *T. niger*, *T. sanborni*, or *T. vellardi*.

### Telmatobufo venustus (Philippi)

*Skull*.—The frontoparietals are paired, not fused with the prootics, and extensive, nearly meeting along the midline anteriorly and sutured posteriorly. Anteriorly, the frontoparietals rest on the sphenethmoid; posteriorly they broadly rest on the otoccipitals. The occipital artery passes through a roofed canal on the posterolateral edge of the frontoparietals (Fig. 14). The calcified sphenethmoid extends anterior to the nasals which lie anterolateral to the sphenethmoid, are broadly separated, and comparatively short. The nasals have an elongate maxillary process that does not reach the maxilla. The nasals are not in contact with the frontoparietals.

The maxillary arch is complete. The premaxillae are relatively narrow and bear short, posterodorsally directed alary processes. The *pars palatina* is narrow except medially where it expands slightly forming short palatine processes. The premaxillary teeth (10–12) are long, fang-like, pedicellate, and well-ankylosed to the



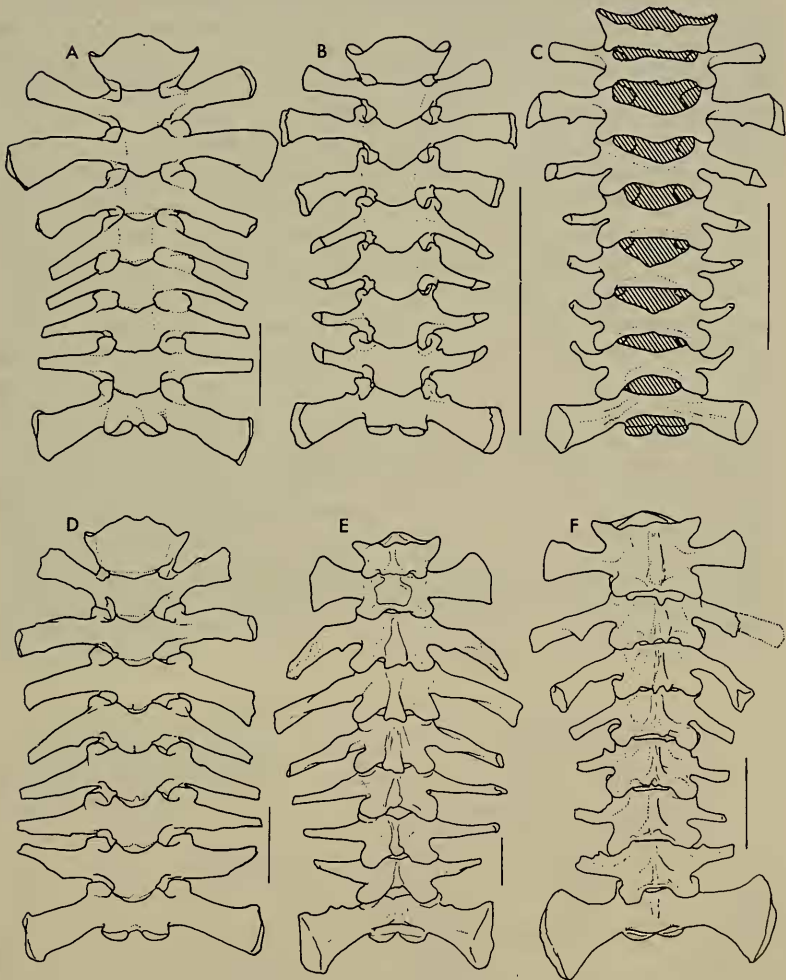


FIG. 13.—Vertebral columns of telmatobiine frogs. (A) *Telmatobius culeus*, KU 135684; (B) *T. hauthali*, KU 72879; (C) *Alsodes gargola*, CHINM 7082; (D) *Batrachophrynus brachydactylus*, SDSNH 46894; (E) *Caudiverbera caudiverbera*, AMNH 51510; and (F) *Telmatobufo venustus*, KU 159811. Lines equal 5 mm.

jaw. The *pars facialis* of the maxilla is moderately deep and restricted to the nasal region. The maxilla bears 34–36 long, pedicellate, well-ankylosed teeth in a row extending to the level of the pterygoid process. The *pars palatina* is relatively narrow anterior and broadens into a pterygoid process posteriorly. The quadratojugal is of moderate size and broadly articulates with the maxilla. The septomaxillae are moderate-sized bones.

The otoccipital is well ossified with low epiotic eminences. The cristae paroticae are short and stocky. An operculum (but no plectrum) is present. The occipital condyles are not stalked and are in median contact. The zygomatic ramus of the squamosal is long and curved. The otic ramus is shorter, turned medially, and bears a broad otic plate which overlays the crista parotica.

The parasphenoid is triradiate. The cultriform process is long and extends anteriorly between the prevomerine odontophores. The parasphenoid alae are oriented at right angles to the cultriform process. Posteromedially, the parasphenoid is emarginate or notched.

The pterygoids are relatively small but massive. The anterior ramus articulates with the pterygoid process of the maxilla as well as overlays the *pars palatina* of the maxilla and nearly contacts the palatine. The median ramus is short but firmly articulates with and overlaps the parasphenoid ala as well as resting against the anterior face of the prootic. The pterygoid does not bear a ventral flange.

The skull anterior to the palatines is not especially short as in *Insuetophrynus*. The palatines are broad, extending from the maxilla onto the edges of the sphenethmoid. The palatines are nearly straight, thin, and bear an anterior flange. The prevomers are relatively small, entire, broadly separated, and bear prominent odontophores between the choanae. The odontophores bear 7-8 long, fang-like teeth in a transverse row.

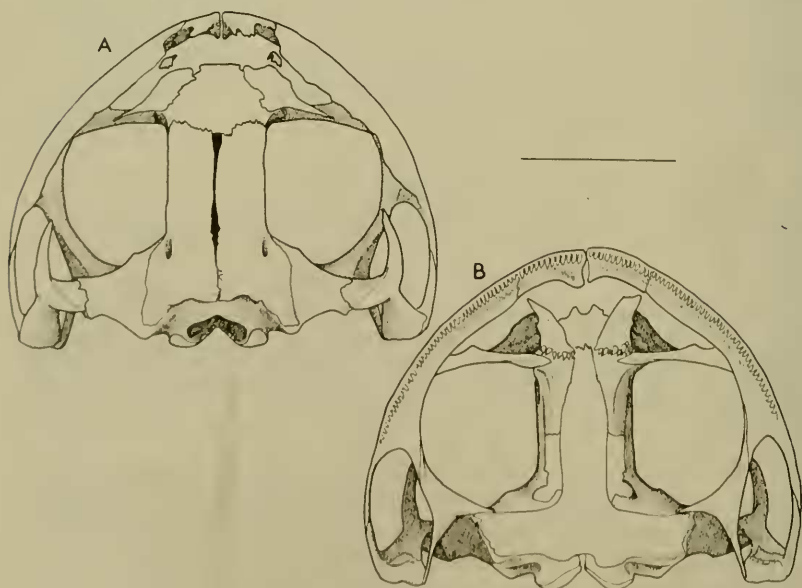


FIG. 14.—Skull of *Telmatobufo venustus* (KU 159811). Line equals 5 mm.

*Vertebral column.*—The cervical and second vertebrae are fused; the column consists of eight procoelous, presacral vertebrae (only seven elements). The cervical cotyles are narrowly separated. The neural arches are nearly completely imbricate and bear low, ridge-like crests. Vertebrae II–IX bear transverse processes without ribs. The transverse processes are broadest on vertebrae II–IV, narrowest on V–VIII; all are narrower than those of the sacrum. The sacral diapophyses are broadly dilated ( $L/W = 1.13\text{--}1.17$ ). The sacro-coccygeal articulation is bicondylar. The anterior end of the coccyx bears some vertebral form. Short transverse processes are present as are two pairs of spinal nerve foramina; the anterior end of the coccyx is slightly inflated (Fig. 13). The posterior edge of the neural arch of the sacrum bears a shelf covering part of the gap between the sacrum and coccygeal neural arch.

*Taxonomic note.*—As Donoso-Barros (1972) pointed out, Philippi's *Bufo venustus* is conspecific with Schmidt's *Telmatobufo bullocki*; the correct combination is *Telmatobufo venustus*, not *Aruncus venustus* as suggested by Donoso-Barros. Donoso-Barros also suggested that *Aruncus valdivianus* Philippi was an earlier name for *Telmatobufo australis* Formas but his argument is untenable for the reasons given by Lynch (1971) in refutation of Gallardo's (1965) parallel proposal.

#### ANALYSIS OF CHARACTERISTICS

Certain characteristics (while often cited) are of little value in demonstrating relationships. These are characteristics having one or more unique character-states. As used here, unique states are those found in only one taxon ("singleton characteristics" of LeQuesne, 1975). Such unique states are quite distinct from character states termed unique by Wilson (1965), Inger (1967), or LeQuesne (1972, 1975). In the group under discussion unique traits include the following:

*Caudiverbera*: Casquing of the skull; contact between frontoparietals and nasals; broad parietal-squamosal contact.

*Telmatobufo*: Fusion of first two vertebrae; sucker-like, ventral mouth of tadpole.

*Insuetophrynus*: Functionally firmisternal pectoral girdle; very small sternum.

*Thoropa*: Elongate, stream-adapted tadpoles.

*Batrachophrynus*: Greatly reduced prevomers; edentulous premaxillae, maxillae, and prevomers; coccygeal flanges.

*Hylorina*: Long digits.

*Atelognathus*: Narrow palatine bones.

Each of the traits listed above demonstrates the distinctiveness

of the genus they characterize but does not contribute data to an exercise devoted to examining similarities.

Nineteen other characteristics are judged to be useful in assessing relationships. Each characteristic is a discontinuous variable and is partitioned into character-states. The character-states are then identified as primitive and derived implying evolutionary direction. The method of establishing evolutionary direction is that used by Tihen (1965) and Lynch (1973, 1975a, 1975b).

For the purposes of analysis, the following putative genera were recognized: (species studied follow in parentheses). *Alsodes* (*A. gargola*, *A. montanus*, *A. monticola*, *A. nodosus*, *A. vanzolinii*), *Atelognathus* (*A. nitoi*, *A. patagonicus*, *A. praebasalticus*, *A. reverberii*, *A. solitarius*), *Batrachophrynus* (*B. brachydactylus*, *B. macrostomus*), *Batrachyla* (*B. leptopus*, *B. taeniata*), *Caudiverbera* (*C. caudiverbera*), *Eupsophus* (*E. roseus*, *E. vertebralis*), *Hylorina* (*H. sylvatica*), *Insuetophrynus* (*I. acarpicus*), *Somuncuria* (*S. somuncurensis*), *Telmatobius* (*T. barrioi*, *T. brevipes*, *T. culeus*, *T. hauthali*, *T. marmoratus*, *T. niger*), *Telmatobufo* (*T. venustus*), and *Thoropa* (*T. lutzi*, *T. miliaris*, *T. petropolitana*).

Of the twenty-three characteristics discussed below, four are rejected as inadequate in assessing relationships. The characteristics are numbered in the same order as they appear in the data matrix (Table 1) and on the cladograms (Figs. 16-17).

1. *Maxillary arch*.—Two character-states are recognized here—a primitive condition in which the maxillary arch is complete (quadratojugal present) and a derived state in which the quadratojugal is lost. The derived state is present in *Atelognathus*, *Batrachyla*, *Hylorina*, *Insuetophrynus*, and *Somuncuria*.

2. *Nasal bones*.—The nasal bones are large and in broad median contact in *Atelognathus*, *Batrachophrynus*, and *Caudiverbera* (Fig. 2). This condition is taken as primitive following Tihen's (1965) reasoning. In *Somuncuria* (Fig. 2), the nasals are small and tenuously in median contact, whereas the bones are small and widely separated in the other genera (Figs. 11, 14). The character-states seen in *Somuncuria* and the other genera are combined into a single derived state.

3. *Exposure of frontoparietal fontanelle*.—In two taxa, *Caudiverbera* and *Telmatobufo*, the frontoparietals are complete covering the frontoparietal fontanelles. In all other taxa, the frontoparietals exhibit appreciable separation medially exposing some expanse termed a fontanelle. The exposure is narrow in *Insuetophrynus* and I have termed the character-state as non-exposed. In all others there is at least a broader exposure anteriorly than posteriorly. In part, exposure of a fontanelle is a function of size in that younger, and smaller, individuals have a greater exposure of the fontanelle

TABLE I.—DATA MATRIX FOR LOWER TELMATOBIINE LEPTODACTYLIDS AND *Pleurodema*.

OTU Code <sup>1</sup>	Characteristics <sup>2</sup>																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
ALSO	0	1	1	0	-1	0	-1	0	1	0	0	1	1	0	0	0	1	1	1
ATEL	1	0	1	0	-1	0	-1	1	1	0	0	1	1	1	1	0	1	1	0
BNUS	0	0	1	0	-1	0	-1	0	0	1	0	0	0	1	0	0	1	1	0
BYLA	1	1	1	0	1	0	0	1	1	-1	1	1	1	0	0	1	1	1	0
CAUD	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0
EUPS	0	1	1	0	-1	1	0	0	0	-1	0	1	1	0	0	0	1	1	0
HYLO	1	1	1	0	0	0	-1	0	0	-1	0	1	1	0	0	0	0	1	0
INSU	1	1	0	0	-1	0	-1	0	1	-1	0	1	1	0	1	0	1	1	1
LIMN	0	1	1	0	1	0	0	0	1	0	0	1	1	0	-1	0	0	1	0
TBUS	0	1	1	0	-1	0	-1	0	1	0	0	1	1	1	0	0	1	1	0
TBUF	0	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
THOR	0	1	1	0	1	0	0	0	1	-1	1	1	1	1	-1	1	1	1	0
SOMU	1	1	0	0	1	0	1	1	1	0	0	1	1	1	0	0	1	1	0
PLEU	1	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	1	1	0

<sup>1</sup> See legend for Fig. 16 (page 40).

<sup>2</sup> See text, p. 28 ff.

than do older and larger examples. As a general corollary adult males have a more extensive fontanelle than do adult females (inasmuch as the latter are larger than the former). Hence, comparisons using specimens of different sizes and sexes may yield spurious results. Only the species of *Atelognathus* can be described as having extensive frontoparietal fontanelles. The fontanelles illustrated by Lynch (1971) for *Batrachyla*, *Hylorina*, and *Thoropa*, while extensive, are of a much lesser magnitude. Partly because of the sexual and size-related variation in this characteristic, I have partitioned it into only two character-states. The primitive character-state is the lack of an exposed fontanelle and is present in only three of the genera (*Caudiverbera*, *Insuetophrynus*, and *Telmatobufo*).

4. *Canal for occipital artery*.—In most frogs, the occipital artery passes dorsally over the posterolateral corner of the frontoparietal. In a number of bufonid and leptodactylid frogs the occipital artery lies in a groove or in an enclosed canal. In *Caudiverbera* and *Telmatobufo*, the occipital artery is enclosed in a bony canal. None of the other species has any suggestion of such a feature. The presence of the enclosed canal is considered to be derived.

5. *Otic element and otic ramus of squamosal*.—*Caudiverbera* exhibits the most marked otic element with the medial extension of the otic ramus of the squamosal to articulate with the parietals. No other genus of telmatobiines approaches this condition. The otic ramus of the squamosal has a small otic plate and curves medially in *Hylorina* and *Telmatobufo*. *Batrachyla* has a narrow otic

plate but the otic ramus is not deflected medially. In *Batrachophrynus* the otic ramus is nearly obsolete but a small otic plate is developed. In the other six genera no otic plate is in evidence although the otic ramus of the squamosal is curved medially in all but *Thoropa*.

Partitioning this characteristic is made more difficult by the lack of comparability between *Caudiverbera* and the other genera. The development of a temporal arcade in *Caudiverbera* has obliterated any medial curvature of the otic ramus of the squamosal; furthermore, the length of the otic ramus in *Caudiverbera* may be partially distorted by the casquing of the skull. The otic ramus is not deflected medially in *Batrachyla* or *Thoropa*; both also have otic rami that are relatively long.

A solution might be to consider the characteristic as two characteristics—the development of an otic plate as one trait and medial deflection or curvature of the otic ramus as a second trait. Such a partitioning is difficult for two reasons: the casquing in *Caudiverbera* and the absence of an otic ramus in *Batrachophrynus*. The latter difficulty could be resolved by considering the otic plate in *Batrachophrynus* to be a homologue of the medially deflected otic ramus such as seen in *Alsodes*, *Eupsophus*, or *Telmatobius*.

Although not entirely satisfactory, I have treated this character-complex as a single characteristic and have divided it into three character-states. The primitive character-state is that in which the otic ramus is medially deflected and an otic plate is developed; in spite of the objections given above, I have characterized *Caudiverbera*, as well as *Hylorina* and *Telmatobufo*, as exhibiting this character-state. The other two character-states are considered independently derived; one in which the otic ramus is long and straight (*Batrachyla* and *Thoropa*) and a second in which the otic ramus is short and curved medially (other six genera).

6. *Pars palatina of premaxilla*.—Medially, a palatine process is developed on the *pars palatina* of the premaxilla. In *Batrachophrynus* and *Caudiverbera*, the *pars palatina* is long; the element is slightly shorter in *Eupsophus* and *Telmatobufo* and is markedly shorter in all other genera. A short *pars palatina* is considered to be primitive and a lengthened element, derived. I have not considered the difference in length between that of *Batrachophrynus* and *Telmatobufo* sufficient to warrant recognition of three character-states.

7. *Pterygoid process of the maxilla*.—Although the *pars palatina* of the maxilla narrows perceptibly posterior to the end of the maxillopterygoid junction in all species examined, only some species have an increase in breadth of the *pars palatina* anterior to the end of the maxillopterygoid junction. A narrow pterygoid process is developed in *Batrachyla*, *Eupsophus*, and *Thoropa* (see figures in

Lynch, 1971). In *Caudiverbera* and *Telmatobufo* a much wider process is developed, and a broad ventral suture develops between the process and the pterygoid. In the other six genera the maxilla tapers gradually or rather abruptly but no process is developed. The strengthened maxillopterygoid junction in *Caudiverbera* and *Telmatobufo* is considered to be derived, as is the absence of a pterygoid process.

8. *Maxillopterygoid overlap*.—The anterior ramus of the pterygoid rests on the dorsal surface of the palatal shelf of the maxilla. In *Atelognathus* and *Batrachyla* the anterior end of the pterygoid extends anteriorly to about mid-orbit; in *Eupsophus* and *Hylorina* it extends considerably more anteriorly and perceptibly less than in *Alsodes*, *Batrachophrynus*, *Caudiverbera*, *Insuetophrynus*, *Telmatobius*, *Telmatobufo*, and *Thoropa*. I have recognized only two character-states; a derived condition for *Atelognathus* and *Batrachyla*, and a primitive condition in the other nine genera.

9. *Articulation of median ramus of pterygoid*.—The median ramus of the pterygoid articulates against the anteroventral surface of the prootic and may or may not contact the anterolateral edge of the parasphenoid ala. The character-state in which the pterygoid and parasphenoid are in contact (*Batrachophrynus*, *Caudiverbera*, *Eupsophus*, *Hylorina*, and *Telmatobufo*) is coded primitive; that seen in the other six genera is derived.

10. *Length of cultriform process of parasphenoid*.—The anterior ramus of the parasphenoid (cultriform process) is very long in *Caudiverbera* and *Telmatobufo*; in each the tip separates both the palatines and prevomers. The element is nearly as long in *Batrachophrynus*. In *Alsodes*, *Atelognathus*, and *Telmatobius*, the cultriform process is noticeably shorter but much longer than that in *Batrachyla*, *Eupsophus*, *Hylorina*, *Insuetophrynus*, and *Thoropa*. The greatest morphological hiatus is between the second and third groups, but I have separated the characteristic into three character-states. The first and third are treated as equally and independently derived from the second.

11. *Separation of occipital condyles and intercotylar separation*.—The occipital condyles are not stalked and narrowly separated in all but two genera, *Batrachyla* and *Thoropa*. In both, the occipital condyles, while not as markedly stalked as seen in eleutherodactyline telmatobiines, are feebly stalked and very widely separated. In the other nine genera, the occipital condyles are more closely juxtaposed. The more lateral position of the occipital condyles in *Batrachyla* and *Thoropa* is reflected in their widely separated cervical cotyles (type I of Lynch, 1971, concave atlas of Gallardo, 1961, 1965). In *Caudiverbera* and *Telmatobufo* the occipital condyles are nearly confluent and the cervical cotyles are narrowly separated

(type II of Lynch, 1971; convex atlas of Gallardo, 1961, 1965). In *Alsodes*, *Atelognathus*, *Batrachophrynus*, *Eupsophus*, *Hylorina*, *Insuetophrynus*, and *Telmatobius* the condyles (and cervical cotyles) are somewhat more separated and may approach the condition described as type I (see Figs. 4 and 13). Barrio (1970) characterized the atlas of *Insuetophrynus* as concave (type I) but his illustrations and my specimens require a characterization as type II. The primitive condition is type II, the derived condition, type I.

12. *Neural arches*.—The neural arches are completely imbricate in *Caudiverbera* and *Telmatobufo* (Fig. 13); the arches are imbricate on the anterior half of the vertebral column and non-imbricate on the posterior half in *Batrachophrynus*. In the other eight genera, the neural arches are uniformly non-imbricate (Figs. 5, 6, 13). Imbricate arches are coded as primitive (following Tihen, 1965, but not Trueb, 1973) and non-imbricate arches as derived.

13. *Coccyx*.—Four species exhibit some vertebral form on the anterior end of the coccyx (*Alsodes montanus*, *Batrachophrynus brachydactylus*, *B. macrostomus*, and *Telmatobufo venustus*) but only *Batrachophrynus* and *Telmatobufo* have inflated, neural-arch like anterior ends of the coccyges. The short transverse processes seen in *Alsodes montanus* are similar to those of *Discoglossus*, whereas the modifications of the anterior end of the coccyx in *Batrachophrynus* and *Telmatobufo* more closely resemble the condition seen in *Mertensophryne*, in which vertebral reduction is achieved via deletion through the sacrum. If the condition seen in *Batrachophrynus* and *Telmatobufo* reflects a recent vertebral deletion, we would have an enigmatic situation inasmuch as both have eight presacral vertebrae, the primitive number found in all non-leiopelmatid frogs, because one must argue that the ancestor(s) of *Batrachophrynus* and *Telmatobufo* had nine presacrals.

I have coded the presence of marked vertebral-like modifications of the anterior end of the sacrum (inflated neural arch, large spinal nerve foramina) as primitive and the absence of such modifications as derived.

14. *Omosternum*.—All eleven genera have cartilaginous omosterna and lack endochondral ossifications within the element. In comparing the omosterna, some obvious variations occur. The omosterna of *Caudiverbera* and *Telmatobufo* are short, broad structures (Fig. 15); in *Alsodes* the manubrial portion of the omosternum is more clearly defined (Fig. 15); in *Batrachyla*, *Eupsophus*, *Hylorina*, and *Insuetophrynus*, the omosterna are slightly longer and the manubrial portion equally well-defined or slightly more clearly defined. The omosterna are much more elongate in *Atelognathus*, *Batrachophrynus*, *Telmatobius*, and *Thoropa* (Figs. 8 and 15). No manubrium is developed in *Atelognathus*, *Batrachophrynus*, and



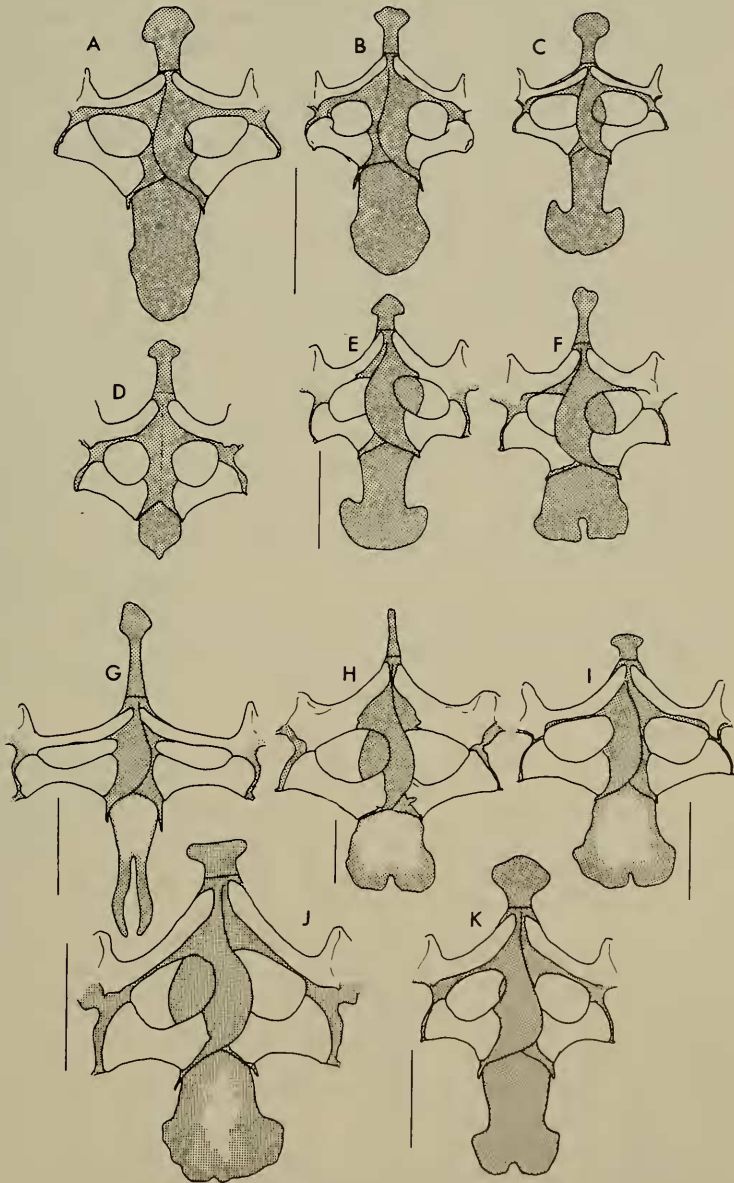


FIG. 15.—Ventral views of pectoral girdles of telmatobiine frogs. (A) *Eupsophus roseus*, KU 160566; (B) *Batrachyla leptopus*, KU 125371; (C) *B. taeniata*, KU 124242; (D) *Insuctophrynus acarpicus*, CHINM 6907; (E) *Hylorina sylvatica*, KU 154546; (F) *Telmatobius brevipes*, KU 131691; (G) *Thoropa miliaris*, KU 92853; (H) *Batrachophrynus brachydactylus*, SDSNH 46894; (I) *Alsodes gargola*, CHINM 7082; (J) *A. montanus*, IBA-UNC 1646/4; and (K) *A. vanzolinii*, KU 162206.

some *Telmatobius* (*barrioi* and *marmoratus*). An ill-defined manubrium is developed in the other *Telmatobius* studied (*brevipes*, *culeus*, *niger*, *sanborni*, and *schneiteri*) as well as in *T. halli* and *T. peruvianus* (Cei, 1962) and in the three species of *Thoropa*. I consider the elongate omosternum to be a derived state, because such a form would allow a more complex site of muscle attachment.

15. *Sternum*.—All taxa in this complex have sterna, but the sternum is markedly reduced in size in *Insuetophrynus* (Barrio, 1970). Endochondral ossifications were noted in *Alsodes*, *Batrachophrynus*, *Caudiverbera*, *Hylorina*, *Telmatobius*, and *Thoropa miliaris*. These ossifications are irregular in shape and in occurrence (most frequent in large individuals) and are completely enclosed by cartilage. Such ossifications represent an advanced character-state over completely cartilaginous sterna and may be ancestral to the character-state(s) where the ossifications form styles and are not enclosed by cartilage. In my previous study of Neotropical leptodactylids (Lynch, 1971) I treated the sternum as exhibiting only two character-states (*viz.*, a primitive state in which the element was cartilaginous with or without calcifications; and a derived state in which the element was more complex having a bony style as well as a cartilaginous portion, the xiphisternum *auctorum*). Heyer (1975) argued that my treatment of the sternum was an oversimplification and used both shape and internal ossifications to partition the character into five character-states.

The most common sternal shape (state A) among the 27 species for which I have data is one in which the sternum broadens posteriorly (Fig. 15I). No obvious indentations allow the recognition of separate metasternum and xiphisternum. The posterior edge is generally weakly indented. This character-state is evident in *Alsodes* (*gargola*, *montanus*), *Batrachophrynus*, *Batrachyla* (*leptopus*), *Caudiverbera*, *Telmatobius* (7 sp. examined), and *Telmatobufo*. A second character-state (state B) is one in which the sides of the sternum gradually narrow (over the anterior  $\frac{1}{2}$  to  $\frac{2}{3}$  of the sternum) and then are markedly inflated (Fig. 15C and E). In this character-state one can easily imagine metasternal and xiphisternal portions of the sternum. Taxa exhibiting this character-state include *Alsodes* (*nodosus*), *Batrachyla* (*taeniata*), *Eupsophus* (*roseus*, *vertebralis*), and *Hylorina*. In *Atelognathus* (5 sp.) and *Insuetophrynus* the margins of the sternum are parallel and there is no posterior inflation of the element (Fig. 8, 15D). I have grouped these two taxa as state C even though the sternum of *Insuetophrynus* is very much shorter than that of *Atelognathus*. The sternum of *Thoropa* is style-like in shape as noted by Heyer (1975); it gradually narrows, lacks the inflated xiphisternal portion, and is deeply indented. The sternum of *Thoropa* (Fig. 15G) resembles

those grouped as state B in that it gradually narrows; it resembles those of state C in that no xiphisternal portion is developed. Accordingly, I consider the sternal apparatus of *Thoropa* to represent a fourth state (D).

Two genera have species exhibiting two character-states. Two species of *Alsodes* exhibit state A and another state B. Cei's (1962) figures suggest that *A. monticola* exhibits state B. One species of *Batrachyla* exhibits state A and another state B. Inasmuch as the posterior edge of the sternum in state A and state B are quite broad, these may be functionally identical. If the characteristic is to be used, each OTU must exhibit a single state; accordingly, state A and state B are combined as the primitive character-state; states C and D are considered independently derived.

16. *Terminal phalanges*.—The terminal phalanges are knobbed in 9 of the eleven genera; the knobbed condition is coded as primitive. The terminal phalanges are T-shaped in *Batrachyla* and *Thoropa*; the T-shaped condition is coded as derived.

17. *Pupil shape*.—In the Patagonian telmatobiines, the pupil is either a vertical slit (primitive character-state: *Caudiverbera*, *Hylorina*, and *Telmatobufo*) or a horizontal slit (derived character-state: other eight genera).

18. *Outer metatarsal tubercle*.—*Caudiverbera* and *Telmatobufo* differ from the other nine genera in lacking an outer metatarsal tubercle. The presence of an outer metatarsal tubercle is considered derived.

19. *Nuptial armature*.—Males of all species for which adults are known have spiny excrescences on the thumb. The excrescences are fine in most species and more coarse in others (Schmidt, 1954; Cei, 1962). Small horny spinules develop on the chest, limbs, and sometimes on the skin of the flanks and back in several *Telmatobius* (Vellard, 1951). The most impressive variation is seen in adult males of *Alsodes* and *Insuetophrynus* where patches of large spines occur on the chest (see illustrations by Barrio, 1970; Cei, 1962; Cei and Roig, 1965; and Gallardo, 1970). A few species of *Telmatobius* have similar nuptial excrescences on the chest, but the spines are small and do not form discrete patches. The presence of discrete pectoral patches is coded as derived; their absence as primitive.

The remaining characteristics have been widely used in the study of leptodactylids but must be rejected for purposes of inferring relationships because either variation is continuous (21, 22) or there is intra-OTU variation in the states (20, 23). State C of trait 15 occurs in a single OTU and does not yield information; trait 15 is used in the analysis but the evolutionary step required to convert A to C is non-informational.

20. *Development of ear*.—Although Grandison (1961) provided a clear cautioning relative to the appropriateness of this characteristic, it has continued to be cited in generic diagnoses as a major characteristic (Gallardo, 1970; Barrio, 1970). In many of the Patagonian telmatobiines the ear is reduced by covering the tympanum and annulus with skin, reduction of the annulus and tympanum, loss of those elements and the cavum tympanicum, and loss of those elements as well as the plectrum. The last and most extreme condition is exhibited by *Alsodes gargola*, *A. montanus*, and *A. monticola*, whereas *A. nodosus* has a complete, albeit concealed, ear (Grandison, 1961). All *Atelognathus* have lost the tympanum, tympanic annulus, cavum tympanicum, and plectrum, as have *Telmatobufo* and several species of *Telmatobius*. The ear is concealed in many other *Telmatobius* and visible in *T. cinereus*. The tympanum is visible externally in *Batrachyla*, *Caudiverbera*, *Eupsophus*, *Hylorina*, and *Thoropa*, concealed in *Insuetophrynus*, and greatly reduced and concealed in *Batrachophrynus*.

The intrageneric variability of this characteristic in *Alsodes* and in *Telmatobius* is the most conclusive reason for rejecting it as a basis for generic distinctions as well as for demonstrating relationships. Within this complex of frogs the limitations of the characteristic are to discussing the distinctions of and relationships of species within a genus.

21. *Transverse processes of vertebrae V–VIII*.—Within the complex of frogs under discussion there is considerable variation in the breadth and orientation of the transverse processes of vertebrae V–VIII (posterior presacral vertebrae of Lynch, 1971, 1973); the greatest difference is between *Atelognathus reverberii* (Fig. 6) and *Batrachophrynus brachydactylus* (Fig. 13). Most species exhibit an intermediate condition of slightly narrowed transverse processes. Broad transverse processes (nearly as broad as the sacral diapophyses—90%) occur in *Batrachophrynus*. *Batrachyla*, *Telmatobius culeus* (Fig. 13), *T. marmoratus*, and *Thoropa* have only slightly narrower transverse processes (ca. 80% of sacral diapophyses width). The transverse processes gradually narrow in *Caudiverbera*; only those of VIII are appreciably narrower than the sacral diapophyses (Fig. 13).

The transverse processes are narrower (58–65%) in *Alsodes*, *Eupsophus*, and *Telmatobius* (*niger* and *schreiteri*); these species have approximately the same degree of narrowness of the transverse processes as seen in most *Atelognathus* (*nitoi*, *patagonicus*, *praebasalticus*, and *solitarius*). The transverse processes are relatively narrow (46–52%) in *Insuetophrynus* and *Telmatobufo*. The transverse processes are obsolete in *Atelognathus reverberi*.

Intrageneric variation in *Atelognathus* and *Telmatobius* suggests

that this characteristic is of little value. *Telmatobius culeus* is a markedly aquatic species and approaches the vertebral form of *Batrachophrynus*, an aquatic genus; narrower transverse processes are found in the less aquatic species of *Telmatobius*. However, broad processes should not be viewed as an aquatic adaptation in view of the narrow processes in the markedly aquatic species *Atelognathus patagonicus* and *Xenopus* as well as the broad processes in the many relatively terrestrial *Eleutherodactylus* and *Leptodactylus*. *Atelognathus solitarius* has narrow transverse processes (comparable to *A. patagonicus*) and is evidently relatively terrestrial (Ceï, 1970a).

22. *Dilation of sacral diapophyses*.—Few Neotropical leptodactylids have dilated sacral diapophyses such as are seen in some Australian leptodactylids and most bufonids. The Patagonian leptodactylids are often characterized as having weakly dilated diapophyses, a character-state suggesting intermediacy between dilated and rounded (characterizing most Neotropical taxa). Without quantification, the three verbalized character-states seem discrete. In order to quantify the trait I have used two ratios to describe the degree of dilation. The first is the length (greatest anteroposterior measurement—near lateral edge of diapophysis) divided by the breadth (a point on a line connecting the lateral base of the prezygapophysis and the lateral edge of the sacral condyle to the tip of the diapophysis, at midpoint) as a measure of sacral dilation. For most species I have measured only a single specimen (right and left). Although some taxa are very readily distinguished (*Batrachophrynus* and *Insuetophrynus*—0.48–0.60 compared to *Caudiverbera* and *Telmatobufo*—1.00–1.17), most taxa exhibit intermediate values. Within *Atelognathus* values range from 0.64–0.96 suggesting that the L/D ratio is a continuous variable. The L/D ratio is useful only if the widths of the sacral diapophyses are proportionately equal.

As an alternative, I measured the greatest length (L above) of the diapophysis as well as the least length to produce a GL/LL ratio. This ratio is independent of diapophysis width and may more closely approximate what many of us have attempted to describe using such epithets as “narrow,” “rounded,” “somewhat dilated,” etc. I have data for 21 species. The smallest GL/LL ratio is seen in *Batrachophrynus macrostomus* (1.15), the largest in *Telmatobufo venustus* (2.54). These two species exemplify the character-states described as “rounded or narrow” and “dilated or expanded.” On the basis of these 21 taxa, the GL/LL ratio is a continuous variable. The extremes are readily identified but there seems to be no gap in the values correlating with any two or three character-states. The GL/LL values for five species of *Atelognathus* nearly span the spec-

trum of variation (*A. praebasalticus*, 1.55; *A. reverberii*, 1.62; *A. nitoi*, 2.32; *A. solitarius*, 2.42; and *A. patagonicus*, 2.49).

While computing these values I noted a general inverse correlation between the widths of the transverse processes of vertebrae VI-VIII and the dilation of the sacral diapophyses. The correlation is not significant ( $r = -0.29$ ,  $p > 0.05$ ) for process widths (VI-VIII) and L/D ratio of the sacral diapophyses nor for process widths and the GL/LL ratios ( $r = -0.18$ ,  $p > 0.05$ ).

23. *Humerus of male*.—Gallardo (1970) emphasized the enlarged forelimbs of the male as a generic feature of *Alsodes*. Barrio (1970) characterized *Insuetophrynus* as having enlarged forelimbs and in part used the trait as evidence of a relationship between the two genera. In order to render the trait less subjective, I have redefined it as the development of large *cristae lateralis*, *medialis*, and *ventralis*. Although all species have a moderate to large *crista ventralis*, most do not have large forelimbs. The massive forelimbs correlate with the hypertrophy of the *crista lateralis* and *crista medialis* and are seen in *Alsodes gargola*, *A. montanus*, *A. monticola*, and *A. nodosus* (and probably *A. illotus*, if adult males were available); the condition also occurs in several *Telmatobius* (s.s.), viz., *marmoratus*, *schreiteri*. The humerus of male *Insuetophrynus* resembles that seen in most frogs where the *crista medialis* and *c. lateralis* are insignificant ridges if detectable at all. Intrageneric variation in character-states precludes use of this trait in attempting to show relationships.

#### ANALYSIS OF RELATIONSHIPS

I analysed the relationships using the CLADON programs described by Bartscher (1966). In using this method, I agree with the assumptions set forth by Camin and Sokal (1965). Certainly of paramount importance is the assumption that shared primitive character-states are evidence of relationship, whereas shared derived character-states do not necessarily provide evidence of relationship. I concur with Eaton's (1970) reasoning that derived character-states may be independently acquired whereas primitive character-states cannot be—sharing primitive character-states is a result of inheritance.

Frogs are a morphologically uniform group (Inger, 1967; Trueb, 1973). I am of the opinion that in such groups independent acquisition of derived character-states is probably the rule. Boek's (1963, 1969) work suggests that this is generally true in birds, another morphologically uniform group whose key adaptations have imposed constraints on radiation. This is not to deny all value to derived character-states in inferring phylogeny but to restrict the value of such character-states. Independent acquisition of a de-

rived state is more likely if two taxa share a single derived state than if two taxa share several derived states (a cluster of derived states could be used to infer relationship). Independent acquisition is considered more likely for those characteristics showing low compatibility with other characteristics.

The most parsimonious cladogram for the eleven telmatobiine genera (excluding *Somuncuria*) requires 46 evolutionary steps (Fig. 16). Three suprageneric groups may be identified. One consists of *Caudiverbera* and *Telmatobufo*; the second of *Batrachyla*, *Eupsophus*, *Hylorina*, and *Thoropa*; and the third of *Alsodes*, *Atelognathus*, *Batrachophrynus*, *Insuetophrynus*, and *Telmatobius*. The relationship of *Alsodes*, *Atelognathus*, *Insuetophrynus*, and *Telmatobius* can be expressed with equal parsimony (subcladogram A') by requiring extra steps in characters 14 (omosternum shape) and 19 (nuptial armature). The distribution of genera on the cladogram does not lend credence to the suprageneric arrangements I advocated previously (Lynch, 1971, 1973). No rational argument could be made to include *Batrachophrynus*, *Caudiverbera*, *Telmatobius*, and *Telmatobufo* in suprageneric group without also including *Alsodes*, *Atelognathus*, and *Insuetophrynus*. I (Lynch, 1971) placed *Batrachyla*, *Eupsophus* (*partim*), *Hylorina*, and *Thoropa* in a tribe (Alsodini) but later (Lynch, 1973) advocated separating *Batrachyla* and *Thoropa* as a tribe.

Barrio (1971) and Barrio and Rinaldi de Chieri (1971) suggested that *Limnomedusa* belongs to this complex of genera because *Limnomedusa* differs from all other Leptodactylines in having 26 chromosomes. Bogart (1973a) pointed out that *Adenomera* also has 26 chromosomes weakening Barrio's argument. If *Limnomedusa* is included with the Patagonian telmatobiines in a cladistic analysis, an additional state for character 15 may be employed; the state is shared with *Thoropa*. The cladogram generated for these 12 genera requires 50 steps (Fig. 16). *Limnomedusa* is situated as a sister group to *Hylorina-Eupsophus-Thoropa-Batrachyla*. Four different, equally parsimonious, trees may be generated (see subcladograms A' and B'). Only two evolutionary steps (i.e., derived character-states) link *Limnomedusa* with *Batrachyla* and *Thoropa*; I viewed the linkage as spurious rather than suggestive of relationship.

When *Pleurodema* and *Somuncuria* are also included in the analysis (Fig. 17), the cladogram undergoes considerable configurational change. *Batrachophrynus* is linked with *Caudiverbera* and *Telmatobufo* rather than with *Alsodes*, *Atelognathus*, *Insuetophrynus*, and *Telmatobius*. In the subcladogram I prefer, *Pleurodema* and *Somuncuria* replaced *Batrachophrynus*. *Limnomedusa* remains associated with *Eupsophus* and *Hylorina*. The failure of *Limnome-*

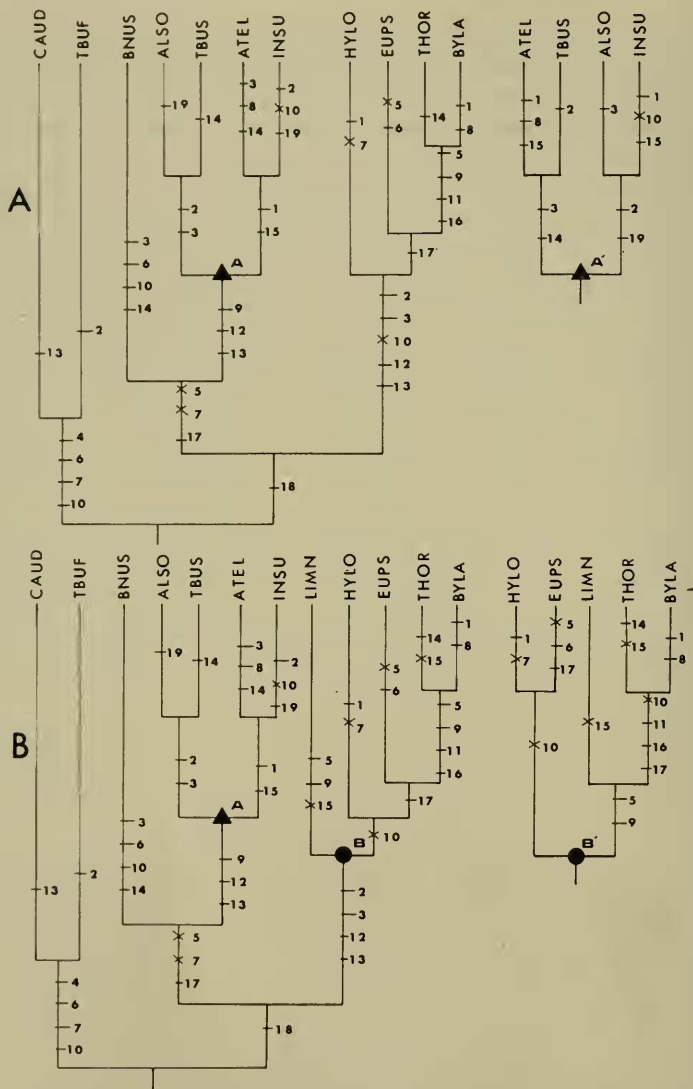


FIG. 16.—(A) Cladogram for 11 OTUs requiring 46 evolutionary steps. The subcladograms, A and A', may be substituted without an increase in evolutionary steps. (B) Cladogram for 12 OTUs requiring 50 evolutionary steps. Subcladograms A and A' and B and B' may be substituted individually or jointly without an increase in evolutionary steps.

Evolutionary steps are numbered (for characteristic numbers refer to pages 28-35) on each lineage; different evolutionary directions are indicated by a horizontal line or an X to the left of the numbered characteristic. OTU identifications are: ALSO (*Alsodes*), ATEL (*Atealogathus*), BNUS (*Batrachophrynus*), BYLA (*Batrachyla*), CAUD (*Caudiverbera*), EUPS (*Eupsophus*), HYLO (*Hylorina*), INSU (*Insuctophrynus*), LIMN (*Liunomedusa*), PLEU (*Pleurodema*), SOMU (*Somuncuria*), TBUF (*Telmatobufo*), TBUS (*Telmatobius*), THOR (*Thoropa*).



*dusa* and *Pleurodema* to associate is suggestive that at least one of them is not properly assigned to the Leptodactylinae.

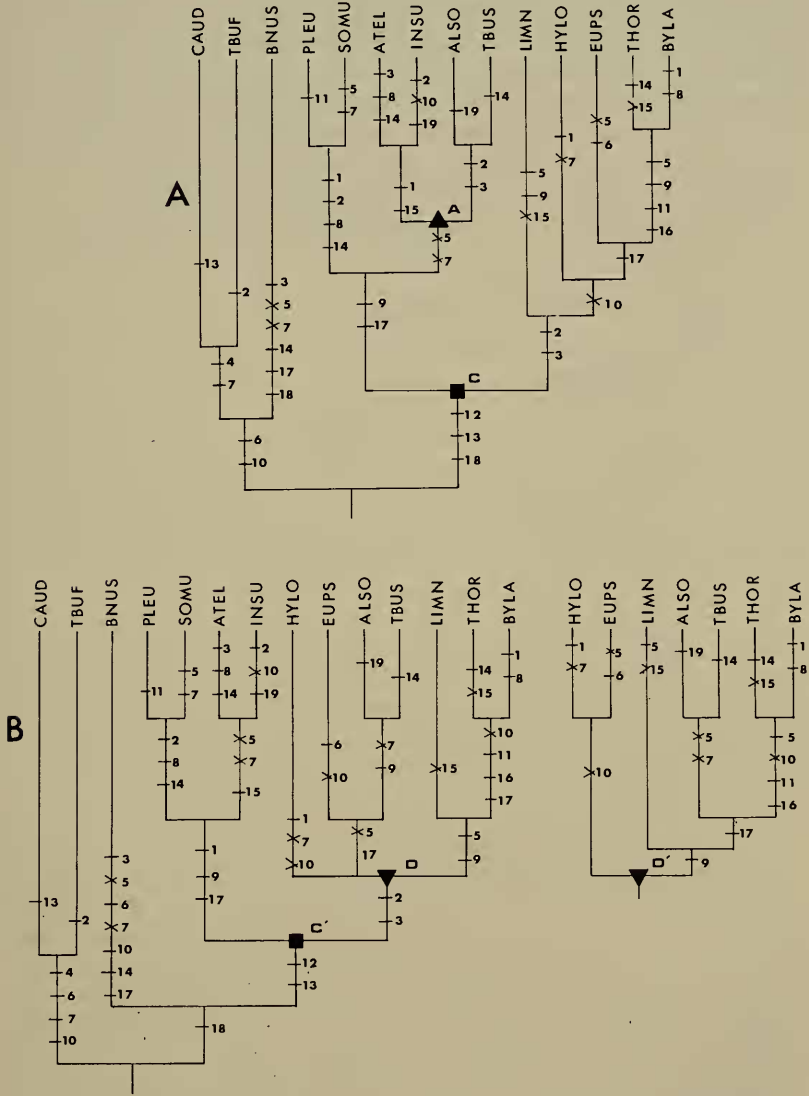


FIG. 17.—(A) Cladogram for 14 OTUs requiring 57 evolutionary steps. Subcladograms A and A' (see Fig. 16A) may be substituted without an increase in evolutionary steps. Subcladograms C and C' (see Fig. 17B) may be substituted without an increase in steps but A and A' may be substituted only when using subcladogram C. (B) Cladogram for 14 OTUs requiring 58 steps. Subcladograms D and D' may be substituted without an increase in steps only when using subcladogram C'. For OTU identifications, see Fig. 16.

Only slightly less parsimonious (58 vs. 57 steps) is a cladogram (Fig. 17) where *Batrachophrynus* is not linked with *Caudiverbera* and *Telmatobufo* but where *Batrachophrynus* is cladistically isolated. The equally parsimonious subcladograms (A', C', D') emphasize characteristics I consider less reliable than those emphasized in the preferred cladogram. All seven evolutionary steps on the *Batrachophrynus* lineage (Fig. 17) are parallelisms. The more parsimonious cladogram (57 steps, Fig. 17) requires six independent character-state shifts for the lineage. The difference is not adequate to convince me that one is to be preferred over the other.

On the basis of these cladograms I proffer the following taxonomic arrangement:

Subfamily TELMATOBIINAE

Tribe CALYPTOCEPHALELLINI Reig

*Caudiverbera*

*Telmatobufo*

Tribe TELMATOBIINI Fitzinger

*Alsodes*

*Atelognathus*

*Batrachophrynus*

*Eupsophus*

*Hylorina*

*Insuetophrynus*

*Linnomedusa*

*Somuncuria*

*Telmatobius*

Tribe BATRACHYLINI Gallardo

*Batrachyla*

*Thoropa*

The three tribes are defined below:

BATRACHYLINI.—Telmatobiine leptodactylids having terrestrial eggs and aquatic larvae, two metatarsal tubercles, horizontal pupils, prevomerine odontophores between the choanae, terminal phalanges T-shaped, leptodactyline ilium type, broad transverse processes of posterior presacral vertebrae, feebly dilated sacral diapophyses, occipital artery not enclosed in bony canal, atlantal cotyles (and occipital condyles) widely separated.

CALYPTOCEPHALELLINI.—Telmatobiine leptodactylids having aquatic eggs and larvae, one metatarsal tubercle, vertical pupils, prevomerine odontophores between the choanae, terminal phalanges knobbed, leptodactyline ilium type, narrow transverse processes of posterior presacral vertebrae, dilated sacral diapophyses, occipital artery enclosed in bony canal, closely juxtaposed atlantal cotyles (and occipital condyles).

TELMATOBIINI.—Telmatobiine leptodactylids having aquatic eggs and larvae, two metatarsal tubercles, horizontal or vertical pupils, prevomerine odontophores between (or slightly posterior to) choanae, terminal phalanges knobbed, leptodactyline ilium type, narrow to broad transverse processes of posterior presacral vertebrae, sacral diapophyses variable (no expansion to broadly dilated), occipital artery not enclosed in bony canal, atlantal cotyles (and occipital condyles) narrowly separated.

The branching sequences (Figs. 16, 17) clearly do not support either of my previous (Lynch, 1971, 1973) arrangements. My 1971 Telmatobiini is clearly polyphyletic, whereas my Alsodini (1971) and Batrachyliini (1973) are monophyletic. Reig's (1960) Calyptcephalellinae is recognizable only if *Telmatobufo* is included. The departures from my earlier arrangements are, in part, results of an improved data base. The improved data base also suggests that certain traits used in my earlier studies (breadth of transverse processes of posterior presacral vertebrae, dilation of sacral diapophyses) were overemphasized. In my previous studies I employed less judicious coding of the variations of the pectoral girdle and did not take advantage of those variations.

Some serological data are available. Cei (1965) demonstrated that *Caudiverbera* is serologically distant from the Ceratophryines *sensu stricto*. He also demonstrated (Cei, 1970b) that *Telmatobufo* is more similar to *Telmatobius* (*sensu stricto*) than to *Caudiverbera* as suggested by Gallardo (1965) and Lynch (1971). Against the background of a much improved anatomical data base, I continue to view *Caudiverbera* as the nearest relative of *Telmatobufo*; thus the morphological and serological data remain incongruent.

Cei's (1970b) study included species here assigned to *Alsodes*, *Atelognathus*, *Caudiverbera*, *Odontophrynus*, *Pleurodema*, *Telmatobius*, and *Telmatobufo*. His data do not support reference of *Telmatobius somuncurensis* to *Pleurodema* but suggest that *Somuncuria* is a member of the complex of genera here termed the lower telmatobiines.

Several authors have asserted relationships between some of the lower telmatobiines on the basis of chromosome data. If *Limnomedusa* is considered a telmatobiine as suggested by Barrio and Rinaldi de Chieri (1971), karyotypic data are available for 12 of the 13 genera (*Batrachophrynus* not studied). Diploid counts are available for 23 species (Barbieri, 1954; Barrio, 1971, 1973; Barrio and Rinaldi de Chieri, 1971; Bogart, 1970; Brum-Zorrilla and Saez, 1968; Cei, 1969b; Formas and Espinoza, 1975; Kuramoto, 1972; Morescalchi, 1973; and Veloso, et al. 1974). The reported diploid counts are: 22 [*Alsodes nodosus* (Bogart, 1970; Brum-Zorrilla and Suez, 1968, Kuramoto, 1972), *Somuncuria somuncurensis* (Cei,

1969b), *Telmatobius* sp of *marmoratus* group (Brum-Zorrilla and Suez, 1968)], 26 [*Alsodes gargola*, *monticola*, and *nodosus* (Barrio and Rinaldi di Chieri, 1971), *Atelognathus patagonicus* and *prae-basalticus* (Barrio and Rinaldi de Chieri, 1971), *A. nitoi* (Barrio, 1973), *A. reverberii* (Cei, 1969b) *Batrachyla antartandica*, *leptopus*, *taeniatus* (Barrio and Rinaldi de Chieri, 1971, Bogart, 1970), *Caudiverbera caudiverbera* (Brum-Zorrilla and Saez, 1968; Formas and Espinoza, 1975; Kuramoto, 1972), *Hylorina sylvatica* (Barrio and Rinaldi de Chieri, 1971), *Insuetophrynus acarpicus* (Barrio and Rinaldi de Chieri, 1971; Bogart, 1970), *Limnomedusa macroglossa* (Barrio, 1971), *Telmatobius barroi*, *ceiorum*, *schreiteri*, *stephani* (Barbieri, 1954; Moresealehii, 1973), *Telmatobufo australis* (Formas and Espinoza, 1975), and *Thoropa milaris* (Bogart, 1970; Brum-Zorrilla and Saez, 1968)], 28 [*Eupsophus vertebralis* (Bogart, 1970)], and 30 [*Eupsophus roseus* (Barrio and Rinaldi de Chieri, 1971; Bogart, 1970)].

Perusal of the literature suggests that intraspecific variation in chromosome number exists in *Alsodes nodosus* (counts of 22 and 26 reported). Alberto Veloso has discovered that the apparent variability is the result of confusing *Alsodes laevis* (Philippi), *A. montanus* (Lataste), and *A. nodosus* (Duméril and Bibron); the first two have diploid counts of 26. Intrageneric variation exists in *Alsodes* (*nodosus* with 22, *gargola* and *monticola* with 26), *Eupsophus* (28 or 30), and *Telmatobius* (22 or 26).

Bogart (1973a) and Moresealechi (1973) have pointed out that numbers of chromosomes relate only a small part of the information in a karyotype. Both authors argue that the 26 chromosome karyotype is primitive among the non-arehaie frog families. The taxa listed above (having 26 chromosomes) may be divided into three groups on the basis of numbers of large and small chromosomes and the magnitude of the size difference between large and small chromosomes.

The most common is one in which there are clearly five large and eight small chromosomes. This pattern is seen in *Atelognathus*, *Batrachyla*, *Hylorina*, *Insuetophrynus*, *Telmatobius*, and *Thoropa*. Barrio and Rinaldi de Chieri (1971) suggested that this pattern is exhibited in *Alsodes* as well but their figure of a karyotype of *A. nodosus* is not convincing. Their figure seems to agree with the figures and data provided by Bogart (1970) and Kuramoto (1972) (six large chromosomes) except that the latter recorded only 11 pairs of elements. The pattern of five clearly large and eight clearly small chromosomes is also seen in the Grypiseines *Cyclorhamphus* and *Zachaenus* (Becak, Denaro, and Becak, 1970; Bogart, 1970).

*Caudiverbera* and *Telmatobufo* have six large chromosomes and seven small ones (Formas and Espinoza, 1975; Kuramoto, 1972) but

the large and small chromosomes are not so clearly defined as in the previous group. The reports for *Alsodes nodosus* by Bogart (1970) and Kuramoto (1972) clearly demonstrate six large chromosomes. Barrio and Rinaldi de Chieri's (1971) figures substantiate this interpretation.

The three remaining species exhibit a karyotype of 26, 28, and 30 chromosomes with a gradual decrease in size from pair 1 to 13, 14, or 15; the decrease is most obvious in *E. roseus* but in *E. vertebralis* one could argue that six large pairs and eight small pairs are found.

In perusing the literature one finds that the Odontophrynines have a karyotype with gradual decrease in chromosome size (Becak, Denaro, and Becak, 1970; Bogart, 1967), as do the Elosiines (Becak, 1968; Bogart, 1970; Denaro, 1972; and de Lucca and Jim, 1974), the leptodactylines (Becak, 1968; Becak, Denaro, and Becak, 1970; Bogart, 1973*b*, 1974), and the eleutherodactylines (Bogart, 1973*b*; de Lucca, Jim, and Foresti, 1974; and de Lucca and Jim, 1974).

*Ceratophrys* (and *Chacophrys*) have either five large and eight small chromosomes (Becak, Denaro, and Becak, 1970; Bogart, 1967) or six large and seven small chromosomes (Morescalchii, 1967). *Lepidobatrachus* have six large and seven small chromosomes (Barrio and Rinaldi de Chieri, 1970; Bogart, 1967). If studies of *Pelobates* and *Scaphiopus* are indicators (Bogart, 1971; Morescalchii, 1967), the level of importance of five vs. six large chromosomes may be generic or subgeneric. However, it seems injudicious to assert that chromosome counts or relative sizes of chromosomes provide critical evidence for subfamily or tribe assignments as suggested on occasions by Barrio and Rinaldi de Chieri (1971), Becak (1968), Bogart (1973*a*), and Morescalchii (1973).

The conclusions reached here require comparison with the recent paper by Heyer (1975), who used Felsenstein's combinatorial method to produce phylogenetic trees; although he argued repeatedly that he embraces the philosophical principles of Hennig (1966), he does so only in part. Heyer rejects the view that shared primitive character-states are evidence of relationship and asserts that only shared derived character-states are evidence of relationship. Hennig (1966) argued that all derived character-states (apomorphies) are not equally usable; only synapomorphies provide evidence of relationships (convergences do not). Heyer seems to agree with Hennig (1966:121-22) in initially assuming that all apomorphies are synapomorphies but at this point he seriously breaches with Hennig because Hennig (1966) attempts to test each trait and then rejects any that are not "proven" synapomorphies (Schlee, 1969). As Schlee (1969) pointed out, the efforts to "prove"

synapomorphies tend to greatly reduce the number of characters employed. As is abundantly evident in Heyer's work, no reduction of traits occurs between his character analysis and his analysis of relationships. As he points out (p. 38), convergence (non-synapomorphies) is quite common. I thus submit that Heyer's (1975) study embraces Hennig's philosophical principles only superficially.

Criticism of Heyer's arrangement is difficult because he does not provide a final tree. His penultimate tree (Heyer, 1975:30-31, fig. 9) was modified by moving *Caudiverbera* from the cecropine (*sic*) branch to the telmatobine branch with attendant increases in convergencies in two traits. His operational basis of a "good phylogeny" involves: 1) reductions in steps reducing convergencies; 2) increases of numbers of monothetic clusters; 3) increase in numbers of unique state appearances; and 4) maximizing the numbers of derived states in any clusters. Moving *Caudiverbera* increases the number of convergences (traits 1 and 14) and reduces the number of unique appearances (-trait 43) but does not link *Caudiverbera* with the other four genera because *Caudiverbera* shares no apomorphy with *Batrachyla*-*Batrachophrynus*-*Eupsophus*-*Telmatobius*. The action does eliminate convergences in traits 16 and 50 but does not increase the number of monothetic clusters (one lost, one gained). Heyer argued (p. 36) that this action "maximizes monothetic clusters and numbers of states within clusters." Although moving *Caudiverbera* to the telmatobine section improves the congruence of Heyer's arrangement and mine it does not appear consistent with Heyer's operational basis.

We also differ in the placement of *Thoropa*. Heyer placed the genus in his grypiscine group whereas I consider *Thoropa* a close ally of *Batrachyla*. Heyer admits that his grypiscine group is one of the weakest points of the phylogeny because the grypiscine group does not form sister-groups and is a nonmonothetic cluster. Heyer argued (p. 35) that "The best test for the validity of the five proposed groupings at present is to see if the five groupings make sense biogeographically." To use biogeographic data to test the phylogeny which is to be analyzed biogeographically is one of the more simple examples of circular reasoning. Heyer later asserted that the grypiscines are closely related—"All grypiscines are found in forested habitats and further, eight of the genera are adapted to forest stream life in *one way or another* (*italics mine*). It is this overall forest stream adaptational complex that convinces me that the grypiscines are a natural unit." Exactly how "*one way or another*" (implying various) leads to "overall forest stream adaptational complex" escapes me. I can only conclude that the argument of relationship stems from some biogeographic interference with systematics.

Using Heyer's data, *Thoropa* shares 13 traits with *Batrachyla*, 10 with *Cycloramphus* and *Zachaenus*, 9 with *Hylodes*, 8 with *Crossodactylus*, 7 with *Megaelosia*, and 6 with *Paratelmatobius*. In Heyer's dendrogram, *Thoropa* clusters with the elosiines on the basis of 3 traits. If *Thoropa* is moved to the telmatobine branch (where it pairs with *Batrachyla*), the two form a cluster on the basis of 7 traits. The two branches with the telmatobine group [(*Batrachyla*-*Thoropa*; 7 trait cluster) (*Batrachophrynus*-*Eupsophus*-*Telmatobius*; 4 trait cluster)] cluster on the basis of 6 traits. This arrangement seems to improve the maximizing of states within clusters (Heyer's operational basis number 4) for the telmatobines and also the grypiscines.

At least some of the differences between the arrangement proposed by Heyer (1975) and that advocated here stem from Heyer's character-state coding and from the broader data base used here. Heyer coded at least some genera on the basis of statements made in Lynch (1971) but for some traits (e.g., sternum ossification) divided the characteristics into character-states that could not be coded from the statements in Lynch (1971); thus Heyer (1975:51, Table B) recorded three character-states for the sternum in *Batrachophrynus*, *Caudiverbera*, *Eupsophus*, and *Telmatobius*, whereas all four genera exhibit the same character-state.

#### DISCUSSION

Schaeffer's (1949) early Tertiary Patagonian leptodactylid frog community consists of at least three elements. *Caudiverbera* is represented and, if my earlier (1971) assertions are correct, *Neoprocoela* may represent a *Batrachophrynus* or *Telmatobufo* ancestor. The third element is Schaeffer's "Eupsophus species." This element may be one or more of the several telmatobiine genera of the tribe Telmatobiini. This particular assemblage of fossils serves as strongly circumstantial evidence of the antiquity and greater past distribution of the primarily austral biocenotic frog community. Seven of the genera are now restricted to central and southern Chile, including the putatively most primitive genera (*Caudiverbera* and *Telmatobufo*). The six genera radiating out from central Chile include the patagonian *Ateolagnathus* and *Somuncuria*, the Andean *Batrachophrynus* and *Telmatobius*, *Thoropa* on the forested mountains of southeastern Brasil, and *Limnomedusa* in the marshes of Uruguay and adjacent Argentina and Brasil. Thus all of the so-called lower telmatobiines are distributed in areas of high (55+) equability (Lynch, 1971). The distributions of the Elosiinae, Grypiscini, and Odontophrynini are also encompassed entirely or in large part by areas of high equability. The stem

genera of the Ceratophryinae and Leptodactylinae also lie within the high equability region of South America. I think that the congruence of distributions of primitive leptodactylids and high equability is not spurious but rather reflective of an ancient fauna and its ancient climate.

Although I eschew reliance on a single trait as the basis for a rational classification, additional comment on vertebral counts seems germane in that it lends some support to Heyer's (1975) suggestion of a leiopelmatid origin for the Neotropical leptodactylids. Griffiths' (1963) diphyletic paradigm of anurans hinged on the eight vs. nine presacral vertebral count. Criticism of that paradigm has been extensive and largely is based on the observation of occasional individuals of discoglossids and pelobatids having nine presacral vertebrae (Kluge and Farris, 1969). The sum of available evidence supports the notion that both families are archaic (Lynch, 1973). Of considerable significance is that no member of the co-called advanced families of frogs has ever been suggested to have more than eight presacral vertebrae.

If the ancestors of *Batrachophrynus* and *Telmatobufo* (the two genera exhibiting vertebral form of the coccyx) did indeed have nine presacral vertebrae (as seems to be the inescapable conclusion), it seems judicious to investigate the possibility of a leiopelmatid origin for the lower telmatobiines. The Jurassic leiopelmatids from Patagonia (*Notobatrachus* and *Vieraella*) have free ribs and nine perichordal presacral vertebrae which in conjunction with an assortment of trivial and less definitive features allow their association with *Ascaphus* and/or *Leiopelma* (Estes and Reig, 1973). The hypothesized presacral vertebral counts for ancestral telmatobiines provides the first evidence of nine presacral vertebrae in advanced frogs and provides some evidence for a leiopelmatid connection independent of a paradigm involving pelobatids. No evidence of free or ankylosed ribs is available for any advanced frog family (Lynch, 1973; however, see Kluge and Farris, 1969, for another view), but the centra of the immature *Atelognathus reverberii* appear to be stegochordal (as also appears to be the case in *Alsodes*, the other *Atelognathus*, and *Insuetophrynus*). The coincidence of non-holochochordal centra and nine presacral vertebrae in ancestral telmatobiines is strongly suggestive of a hypothetical ancestor intermediate between leptodactylids and leiopelmatids; the Cretaceous frog fauna of Patagonia may resolve the question but the significance of Neotropical leptodactylids in the reigning paradigms of frog evolution (Lynch, 1973; Savage, 1973) seems certain to increase substantially.



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Abbreviations for collections used throughout the text are:

AMNH	American Museum of Natural History
BMNH	British Museum (Natural History)
CHINM	Colección Herpetológica del Instituto Nacional de Microbiología (Universidad de Buenos Aires)
FMNH	Field Museum of Natural History
IBA-UNC	Instituto Biología Animal, Universidad Nacional de Cuyo
KU	Museum of Natural History, The University of Kansas
MCZ	Museum of Comparative Zoology, Harvard University
SDSNH	San Diego Natural History Museum
UMMZ	University of Michigan Museum of Zoology

## SUMMARY

Six of the seven species heretofore termed "extra-andean" *Telmatobius* are transferred to a new genus, *Atelognathus*, generotype *Batrachophrynus patagonicus* Gallardo. The six species of *Atelognathus* are *A. grandisonae* (Lynch), *A. nitoi* (Barrio), *A. patagonicus* (Gallardo), *A. praebasalticus* (Cei and Roig), *A. reverberii* (Cei), and *A. solitarius* (Cei). The seventh extra-andean *Telmatobius* is placed in a new genus, *Somuncuria*, generotype *Telmatobius somuncurensis* Cei, 1969, intermediate between *Atelognathus* and *Pleurodema*.

Osteological data for *Alsodes gargola*, *A. montanus*, *Batrachophrynus brachydactylus*, *Insuetophrynus acarpicus*, *Telmatobius barrio*, *T. brevipes*, *T. culeus*, *T. niger*, and *Telmatobufo venustus* permit and prompt a reevaluation of the relationships of the leptodactylids previously placed in the tribes Alsodini, Batrachylini, and Telmatobiini of the subfamily Telmatobiinae. Thirteen genera of lower telmatobiines are recognized.

The monotypic genus *Caudiverbera* and the genus *Telmatobufo* (*australis* and *venustus*) are placed in the tribe Calyptocephalellini. Two genera, *Batrachyla* and *Thoropa* are placed in the tribe Batrachylini. Nine genera, *Alsodes*, *Atelognathus*, *Batrachophrynus*, *Eupsophus*, *Hylorina*, *Insuetophrynus*, *Limnomedusa*, *Somuncuria*, and *Telmatobius*, are placed in the tribe Telmatobiini. The content and distribution of each of the thirteen genera are summarized as follows:

#### Batrachylini

*Batrachyla* Bell. Three species (*antartandica*, *leptopus*, and *taeniata*) in central and southern Chile (and adjacent Argentina).

*Thoropa* Cope. Three species (*lutzi*, *miliaris*, and *petropolitana*) in the mountains of southeastern Brasil.

#### Calyptocephalellini

*Caudiverbera* Laurenti. One species (*caudiverbera*) in central and southern Chile. Tertiary fossils in central and southern Argentina.

*Telmatobufo* Schmidt. Two species (*australis* and *venustus*) in southern Chile.

#### Telmatobiini

*Alsodes* Bell. Seven species (*gargola*, *illotus*, *laevis*, *monticola*, *montanus*, *nodosus*, and *vanzolinii*) in central and southern Chile (and adjacent Argentina). *A. illotus* is doubtfully distinguished from *A. nodosus*; the inclusion of *A. laevis* is based on discussions with my colleague Alberto Veloso. *Eupsophus vanzolinii* named by Donoso-Barros (1974) is here transferred to *Alsodes*.

*Atelognathus* Lynch. Six species (*grandisonae*, *nitoi*, *patagonicus*, *praebasalticus*, *reverberii*, and *solitarius*) in south-central Argentina and extreme southern (austral) Chile.

*Batrachophrynus* Peters. Two species (*brachydactylus* and *macrostomus*) in the Andes of central Perú.

*Eupsophus* Fitzinger. Two species (*roseus* and *vertebralis*) in southern Chile. Two Peruvian species formerly associated with this genus belong to other genera: *peruanus* Peters in the genus *Phrynopus* and *juninensis* Shreve in the genus *Telmatobius* (see below). The fossils (Oligocene, Chubut, Argentina) reported by Schaeffer (1949) require study in light of data now available and cannot be confidently assigned to *Eupsophus*.

*Hylorina* Bell. One species (*sylvatica*) in southern Chile.

*Insuetophrynus* Barrio. One species (*acarpicus*) in southern Chile.

*Limnomedusa* Fitzinger. One species (*macroglossus*) in southern Brasil, Uruguay, and adjacent Argentina.

*Somuncuria* Lynch. One species (*somuncurensis*) from the Somuncura Plateau in south-central Argentina.

*Telmatobius* Wiegmann. Twenty-five species (*albiventris*, *arequipensis*, *atacamensis*, *barrioi*, *brevipes*, *brevirostris*, *ceiorum*, *cinereus*, *crawfordi*, *culeus*, *halli*, *hauthali*, *ignavus*, *intermedius*, *jelskii*, *juninensis*, *marmoratus*, *niger*, *oxycephalus*, *peruvianus*, *rimac*, *simonsi*, *stephani*, *vellardi*, and *verrucosus*) in the Andes from north-central Ecuador to northern Argentina and Chile. *Telmatobius juninensis* (Shreve), new combination, is a webless species and thus initially seems very different from *Telmatobius*. Web reduction is most marked in this species but webbing is reduced in Vellard's (1951) *latirostris* group (the semi-terrestrial, northern species). Data are too limited to suggest that Vellard's groupings are defensible or that *juninensis* is a member of the *latirostris* group. Osteologically, *juninensis* agrees with *Telmatobius* rather than *Alsodes* or *Eupsophus*.

The lower telmatobiines are distributed in high-equability South America. This austral biocenotic frog community was probably more widely distributed in the early Tertiary. The antiquity of this assemblage is inferred from Schaeffer's Eocene-Oligocene fauna in Patagónia. The presence of vertebral form of the coccyx in *Batrachophrynus* and *Telmatobufo* means that their ancestor(s) had nine presacral vertebrae. These data in conjunction with apparent stegochordal centra in *Atelognathus* suggest the likelihood of a leiopelmatid ancestry for the lower telmatobiines. The chain of data consisting of: 1) the central position of leptodactylids in models of frog phylogeny, 2) Eocene-Oligocene lower telmatobiine frog community; 3) nine presacral vertebrae and non-holochordal centra in lower telmatobiines; and 4) Patagonian Jurassic leiopelmatids is suggestive of the antiquity and autochthony of much of the Neotropical frog fauna.

#### RESÚMEN

Seis de las siete especies definidas en este trabajo como *Telmatobius* "extra-andinos," son transferidos a un nuevo género, *Atelognathus*, cuyo génerotipo es *Batrachophrynus patagonicus* Gallardo. Esas seis especies de *Atelognathus* son: *A. grandisonae* (Lynch), *A. nitoi* (Barrio), *A. patagonicus* (Gallardo), *A. praebasalticus* (Cei y Roig), *A. reverberii* (Cei), y *A. solitarius* (Cei). La séptima entidad extra-andina de *Telmatobius* es colocado en un nuevo género, *Somuncuria*.

El análisis de la osteología de *Alsodes gargola*, *A. montanus*, *Batrachophrynus brachydactylus*, *Insuetophrynus acarpicus*, *Telmatobius barrioi*, *T. brevipes*, *T. culeus*, *T. niger*, y *Telmatobufo venustus* permite y conduce a una reevaluación de las relaciones de los leptodactylidos que anteriormente habían sido colocados en

les tribus Alsodini, Batrachylini, y Telmatobiini de la subfamilia Telmatobiinac. Trece géneros de telmatobiinos inferiores son reconocidos.

El género monotípico *Caudiverbera* y el género *Telmatobufo* (*australis* y *venustus*) son colocados en la tribu Calyptocephalellini. Dos géneros, *Batrachyla* y *Thoropa*, se colocan en la tribu Batrachylini. Otros nueve géneros, *Alsodes*, *Atelognathus*, *Batrachophrynus*, *Eupsophus*, *Hylorina*, *Insuetophrynus*, *Limnomedusa*, *Somuncuria*, y *Telmatobius*, son colocados en la tribu Telmatobiini. La diversidad específica y la distribución de los trece géneros se expresa como sigue:

#### Batrachylini

*Batrachyla* Bell. Tres especies (*antarctandica*, *leptopus*, y *taenitata*) en el Centro y Sur de Chile y regiones adyacentes de Argentina.

*Thoropa* Cope. Tres especies (*lutzi*, *miliaris*, y *petropolitana*) in las montañas del sudeste del Brasil.

#### Calyptocephalellini

*Caudiverbera* Laurenti. Una especie (*caudiverbera*) en Chile Central y Sur. Fósiles terciarios se encuentran en el Centro y Sur de Argentina.

*Telmatobufo* Schmidt. Dos especies (*australis* y *venustus*) en el Sur de Chile.

#### Telmatobiini

*Alsodes* Bell. Siete especies (*gargola*, *illotus*, *laevis*, *montanus*, *monticola*, *nodosus*, y *vanzolinii*) en el Centro y Sur de Chile y regiones adyacentes de Argentina. *Alsodes illotus* es dudosamente distinguible de *A. nodosus*. La inclusión de *A. laevis* se basa en discusiones sostenidas con mi colega Alberto Veloso.

*Atelognathus* Lynch. Seis especies (*grandisonae*, *nitoi*, *patagonicus*, *praehasalticus*, *reverberii*, y *solitarius*) se encuentran en el Centro-sur de Argentina y en Chile austral.

*Batrachophrynus* Peters. Dos especies (*brachydactylus* y *macrostomus*) en los Andes Centrales de Perú.

*Eupsophus* Fitzinger. Dos especies (*roseus* y *vertebralis*) en el Sur de Chile. Dos especies peruanas anteriormente asociadas a este género pertenecen a otra entidad: *peruanus* Peters al género *Phrynopus*, y *juninensis* Shreve al género *Telmatobius* (véase abajo). Los fósiles (del Oligoceno del Chubut, Argentina) descritos por Schaeffer (1949) requieren un reestudio a la luz de las nuevas informaciones disponibles; por ello no puede ser confiadamente asignado a *Eupsophus*.

*Hylorina* Bell. Una especie (*sylvatica*) en la región Sur de Chile.

*Insuetophrynus* Barrio. Una especie (*acarpicus*) en la región Sur de Chile.

*Limnomedusa* Fitzinger. Una especie (*macroglossa*) en el sudeste Brasileño, Uruguay, y la región adyacente de Argentina.

*Somuncuria* Lynch. Una especie (*somuncurensis*) en la meseta basáltica de Somuncura en el Centro-sur de Argentina.

*Telmatobius* Wiegmann. Veinticinco especies (*albiventris*, *arequipensis*, *atacamensis*, *barrioi*, *brevipes*, *brevirostris*, *ceiorum*, *cinereus*, *crawfordi*, *culeus*, *halli*, *hauthali*, *ignavus*, *intermedius*, *jelskii*, *juninensis*, *marmoratus*, *niger*, *oxycephalus*, *peruvianus*, *rimac*, *simonsi*, *stephani*, *vellardi*, y *verrucosus*) en los Andes desde la región Norcentral de Ecuador hasta el Norte de Argentina y Chile. *Telmatobius juninensis* (Shreve), nueva combinación, es una especie sin membrana interdigital y en consecuencia puede considerarse muy diferente de la mayoría de los *Telmatobius*. La reducción de la membrana es muy marcada en esta especie, sin embargo la membrana está también reducida en el grupo *latirostris* de Vellard (1951) (la especie nortina semiterrestre). La información es demasiado limitada como para sugerir que el agrupamiento hecho por Vellard es sostenible o que *juninensis* es un miembro del grupo *latirostris*. Osteologicamente, *juninensis* concuerda con *Telmatobius* antes que con *Alsodes* o con *Eupsophus*.

Los telmatobiinos inferiores se distribuyen en regiones de alta constancia termica relativa en Sud América. Esta comunidad de sapos australes estuvo probablemente más ampliamente distribuida en los comienzos del Terciario. La antigüedad de este conjunto es inferida desde la fauna patagónica del Eoceno-Oligoceno de Schaeffer. La presencia de un coccyx con forma de vertebra en *Batrachophrynus* y en *Telmatobufo* significa que sus antecesores tuvieron nueve vertebrae presacrales. Estos datos, en conjunto con la clara presencia de centro stegochordal en *Ateolognathus* sugiere la posibilidad de un antecesor leiopelmátido para los telmatobiinos inferiores. La secuencia de información consiste en: 1) la posición central de los leptodactylidos en los modelos de la filogenia de los anuros; 2) una comunidad anura de telmatobiinos inferiores en el Eoceno-Oligoceno; 3) nueve vertebrae presacrales y centro non-holochoardal en los telmatobiinos inferiores; y 4) la presencia de leiopelmátidos Jurásicos en la Patagonia es sugestiva de la antigüedad y del endemismo de la mayoría de la fauna de anuros neotropicales.

#### SPECIMENS EXAMINED

*Alsodes gargola* (2) CHINM 7082-83; *Alsodes montanus* (2) IBA-UNC 1646/2, 1646/4; *Alsodes vanzolinii* (1) KU 162247;

*Atelognathus nitoi* (2) CHINM 6875, 6877; *Atelognathus patagonicus* (19) IBA-UNC (18 uncatalogued, identified as 1A-E, 2A-E, 3A-G), KU 80781; *Atelognathus praebasalticus* (1) IBA-UNC 1845/5; *Atelognathus reverberii* (6) IBA-UNC (uncatalogued, identified as 4A-F); *Atelognathus solitarius* (2) IBA-UNC (uncatalogued, identified as 5A-B); *Batrachophrynus brachydactylus* (1) SDSNH 46894; *Batrachophrynus macrostomus* (2) KU 98127-28; *Batrachyla leptopus* (1) UMMZ S-2246; *Batrachyla taeniata* (1) UMMZ S-2247; *Caudiverbera caudiverbera* (5) AMNH 23622, 23958, 24016, 51510, FMNH 9703; *Eupsophus roseus* (3) AMNH 22104, KU 84731, 162204; *Eupsophus vertebralis* (1) KU 162238; *Hylorina sylvatica* (3) BMNH 91.29.17, KU 161407-08; *Insuetophrynus acarpicus* (2) CHINM 6903, 6907; *Limnomedusa macroglossa* (2) KU 92960-61; *Somuncuria somuncurensis* (2) IBA-UNC 2135/7, 2135/8; *Telmatobius barrioi* (1) KU 128880; *Telmatobius culeus* (1) KU 135864; *Telmatobius hauthali* (2) KU 72879, UMMZ S-164; *Telmatobius juninensis* (1) MCZ 24360; *Telmatobius marmoratus* (3) KU 135903, UMMZ 68179(2); *Telmatobius niger* (2) KU 131795-96; *Telmatobufo venustus* (2) KU 159811, 161439; *Thoropa lutzi* (2) KU 92850, 92908; *Thoropa miliaris* (2) KU 92855-56; *Thoropa petropolitana* (1) KU 92862.

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